# Une approche 3D pour comprendre la taphonomie des homininés du site plio-pléistocène de Malapa, Province du Gauteng, Afrique du Sud

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Par Aurore VAL

# UNE APPROCHE 3D POUR COMPRENDRE LA TAPHONOMIE DES HOMININÉS DU SITE PLIO-PLÉISTOCÈNE DE MALAPA, PROVINCE DU GAUTENG, AFRIQUE DU SUD

Sous la direction de Francesco d'Errico, Lucinda Backwell et Lee Berger

Soutenue le 28 Février 2014

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# Titre : Une approche 3D pour comprendre la taphonomie des hominines du site plio-pleistocene de Malapa, Province du Gauteng, Afrique du Sud


## Résumé :

Le site de Malapa a livré les restes de deux homininés, associés aux restes d'autres animaux et datés à 1,98 Ma. Le degré de conservation restes osseux est remarquable dans le contexte des ensembles fossiles plio-pléistocènes retrouvés en grotte. Cela indique une combinaison de processus taphonomiques unique et non-observée dans les sites contemporains de la région. Une approche combinant analyses paléontologique, physique et spatiale des homininés et de la faune associée a été choisie afin d'interpréter la taphonomie de l'ensemble fossile, avec une attention toute particulière portée aux homininés. Des techniques de tomographie et micro-tomographie assistées par ordinateur, combinées à un logiciel de reconstruction virtuelle ont été appliquées afin de créer un modèle en 3 dimensions de la grotte et des deux squelettes d'*Au*. *sediba*. La position initiale dans laquelle les homininés ont été enfouis a été reconstruite. Les résultats indiquent que la majorité du matériel osseux a été accumulée par l'intermédiaire d'un aven-piège. Les carcasses se sont accumulées sous la forme d'un cône de débris, dans une partie profonde du système karstique présentant un accès très limité voire inexistant pour les charognards. Les deux individus ne sont peut-être pas entrés dans la grotte au même moment. Lorsque l'enfouissement a eu lieu, leur décomposition était achevée (disparition et/ou dessiccation des parties molles). Leurs os présentent des indices d'intempérisation, suggérant une période d'exposition avant l'enfouissement d'au moins plusieurs mois. Les insectes sont les principaux agents ayant modifié les restes. Les indices de momification naturelle avant l'enfouissement pour MH1 et MH2 suggèrent la préservation possible de matière organique (peau).



## Mots clés :

Taphonomie osseuse

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# Title : A 3D approach to understand the taphonomy of the early hominins from the plio-pleistocene cave site of Malapa.


## Abstract :

The cave deposits at Malapa have yielded the remains of two extremely well-preserved hominins (*Australopithecus sediba*) and associated fauna, dated to 1.977-1.8 Ma. The state of preservation of the hominins and some of the non-hominin material is remarkable in the context of Plio-Pleistocene fossil assemblages accumulated in caves, and indicates a unique combination of taphonomic processes, not yet observed in contemporaneous cave deposits in the region. A comprehensive approach, including palaeontological, physical, and spatial analyses of the hominins and associated fauna was undertaken to determine, describe and interpret the taphonomy of the faunal material, with particular reference to hominins. An innovative combination of Computed-Tomography (CT), micro-CT scanning and virtual reconstruction techniques was applied to create a 3D model of a selected area of the Malapa cave, with renderings of the two near-complete *Au. sediba* skeletons. The original burial position of the hominins was reconstructed. The results indicate that the majority of the faunal material recovered was most likely accumulated via a natural death trap. Their bodies came to rest in a deep area of the cave system with restricted access to scavengers. Results show that both individuals did probably not enter the cave system at the same time. They reached skeletonization and were slightly weathered before final burial, indicating several years of exposure before burial. Insects proved to be the primary modifiers of the hominin remains. Evidence of natural mummification before burial for MH1 and MH2 suggests the possible preservation of soft tissue.



## Keywords :

Bone taphonomy

Early hominins

3D techniques

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## Declaration

I, Aurore Marie Sophie Val, declare that this PhD thesis is my own, unaided work. It is being submitted for the Degree of Doctor of Philosophy at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any other University.

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Signed on the ……th of July 2013, in Johannesburg.

## Abstract

The cave deposits at Malapa, on the Malapa Nature Reserve, Cradle of Humankind World Heritage Site, Gauteng Province, South Africa, have yielded the remains of two extremely well-preserved hominins (*Australopithecus sediba*) and associated fauna, dated by U/Pb methods and palaeomagnetism to 1.977-1.8 Ma. The state of preservation of the hominins and some of the non-hominin material, characterised by complete and near complete elements, antimeric sets of bones, specimens in articulation, and well-preserved bone surfaces, is remarkable in the context of Plio-Pleistocene fossil assemblages accumulated in caves, and indicates a unique combination of taphonomic processes, not yet observed in contemporaneous cave deposits in the region. A comprehensive approach, including palaeontological, physical, and spatial analyses of the hominins and associated fauna was undertaken to determine, describe and interpret the taphonomy of the faunal material, with particular reference to the holotype and paratype of *Au. sediba*, Malapa Hominin 1 (MH1) and Malapa Hominin 2 (MH2). An innovative combination of Computed-Tomography (CT), micro-CT scanning and virtual reconstruction techniques was applied to create a 3D model of a selected area of the Malapa cave, with renderings of the two near-complete *Au. sediba* skeletons. The original burial position of the hominins was reconstructed, which necessitated the refitting of *ex situ* fossils into *in situ* deposits. The spatial distribution and orientation of the hominin remains illustrate a very low degree of dispersal of the bones, indicative of very little disruption between death and burial, due to an absence of damage by scavengers and possible natural mummification. The very few carnivore-damaged bones and relative abundance of complete and/or articulated specimens, the presence of antimeric sets of bones in the faunal assemblage, as well as the diversity of the faunal spectrum, and the significant percentage of animals with climbing proclivities (such as carnivores and hominins) indicate that the majority of the faunal material recovered was most likely accumulated via a natural death trap. Their bodies came to rest in a deep area of the cave system with restricted access to

scavengers. Skeletons and bones accumulated in a talus cone below a vertical shaft. There, they decomposed, and became buried without major disruption by biotic or abiotic agents. A new forensic approach, referred to as *palaeoforensic taphonomy*, was followed in each step of the taphonomic analysis of the two hominins in order to reconstruct the processes of decay, disarticulation, burial and preservation. Results show that both individuals did probably not enter the cave system at the same time. They reached skeletonization and were slightly weathered before final burial, indicating several years of exposure before burial. Insects proved to be the primary modifiers of the hominin remains, pre- and post-depositional with hide beetles (*Omorgus squalidus*) providing the closest match for some of the fossil modifications observed. Based on the high number of articulated remains, the absence of preferential orientation for the elongated bones and of significant movement of the hominin remains inside the deposit, the debris flow hypothesis that was previously proposed as the principal agent to explain the burial of the hominins and other well-preserved animals is challenged. Evidence of natural mummification before burial for MH1 and MH2 suggests the possible preservation of soft tissue. The innovative 3D techniques applied in this research to conduct the spatial analysis of the fossils proved useful to address taphonomic questions, and will serve as a guide for future excavations of the Malapa *in situ* deposits, especially for locating the missing skeletal elements of MH1 and MH2.

## Résumé

Le gisement fossile de Malapa, situé à l'intérieur de la réserve naturelle de Malapa, dans le Cradle of Humankind (Province du Gauteng, Afrique du Sud), une région reconnue au patrimoine mondial de l'UNESCO, a été découvert en 2008 suite à une campagne d'exploration dirigée par L. Berger et mêlant l'utilisation de Google Earth avec des prospections pédestres classiques. Ce site a livré les restes extrêmement bien préservés de deux homininés, associés aux restes d'autres animaux et datés par U/Pb et paléomagnétisme à 1,98 Ma. Les fossiles d'homininés ont été attribués à un nouveau taxon, *Australopithecus sediba* (du mot sotho signifiant « source, fontaine ») sur la base d'une mosaïque de caractères morphologiques primitifs et dérivés inédite.

Le degré de conservation des homininés et d'une partie de l'ensemble faunique se caractérise par la présence d'os complets et quasi-complets, de sets d'ossements symétriques, de restes articulés et de surfaces osseuses bien préservées, ce qui est remarquable dans le contexte des ensembles fossiles retrouvés en grotte datant du plio-pléistocène. Cela indique une combinaison de processus taphonomiques unique et non-observée dans les sites contemporains de la région. Une approche combinant analyses paléontologique, physique et spatiale des homininés et de la faune associée a été choisie afin de déterminer et d'interpréter la taphonomie de l'ensemble fossile, avec une attention toute particulière portée à l'holotype et au paratype d'*Au*. *sediba*, Malapa Hominin (MH1), un individu jeune et de sexe masculin, et Malapa Hominin 2 (MH2), un individu adulte et de sexe féminin, respectivement. Des techniques innovantes de tomographie et micro-tomographie assistées par ordinateur, combinées à un logiciel de reconstruction virtuelle ont été appliquées afin de créer un modèle en 3 dimensions de la grotte et des deux squelettes d'*Au*. *sediba*. Une partie importante des restes fossiles ont été retrouvés prisonniers dans de blocs de brèche ou sédiments clastiques calcifiés, eux-mêmes déplacés par les mineurs lors de l'exploitation du site pour le calcaire au début du vingtième siècle. La position initiale dans laquelle les homininés ont été enfouis a due être

reconstruite, ce qui a nécessité de déterminer la position dans les dépôts des restes retrouvés *ex situ*.

La distribution spatiale et l'orientation des restes d'homininés illustre un très faible degré de dispersion des os, indiquant très peu de perturbation entre le moment de la chute dans la grotte et le moment de l'enfouissement des restes, ce qui s'explique notamment par l'absence de dommage causé par les charognards et par une possible momification des squelettes. La présence, dans l'ensemble faunique, d'un très petit nombre d'ossements affectés par les carnivores, de nombreux restes complets et/ou articulés, de plusieurs sets d'os symétriques ainsi que la diversité du spectre faunique et le pourcentage important d'animaux doués pour l'escalade, comme les homininés et les carnivores, indiquent que la majorité du matériel osseux a été accumulée par l'intermédiaire d'un aven-piège. Les carcasses se sont accumulées sous la forme d'un cône de débris, en bas d'une faille verticale, dans une partie profonde du système karstique présentant un accès très limité voire inexistant pour les charognards. Après et/ou pendant leur décomposition, les carcasses ont été enfouies sans avoir subi de perturbations majeures causées par des agents biotiques ou abiotiques. Une approche s'inspirant de la « forensic taphonomy » a été suivie à chaque étape de l'analyse taphonomique des homininés afin d'identifier et de décrire l'ensemble des procédés de décomposition, désarticulation, enfouissement et conservation des restes.

Les résultats montrent que les deux individus ne sont peut-être pas entrés dans la grotte au même moment. Lorsque l'enfouissement a eu lieu, leur décomposition était achevée (disparition et/ou dessiccation des parties molles). Leurs os présentent des indices d'intempérisation, ce qui indique une période d'exposition avant l'enfouissement d'au moins plusieurs mois. L'analyse systématique des surfaces osseuses à l'aide d'un microscope optique démontre que les insectes sont les principaux agents ayant modifié les restes, pré- et post-dépositionnellement, comme en attestent les modifications observées sur la surface de certains restes. L'espèce produisant les traces ressemblant le plus à celles observées sur le matériel fossile est *Omorgus squalidus*, un coléoptère

appartenant à la famille des Trogidae. Les indices de momification naturelle avant l'enfouissement pour MH1 et MH2 suggèrent la préservation possible de matière organique (peau). Les techniques 3D appliquées à l'analyse spatiale des fossiles se sont révélées utiles pour adresser des questions d'ordre taphonomique et serviront de guide lors les prochaines fouilles des dépôts en place, particulièrement afin de localiser les restes d'homininés manquants.

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# Chapter 1. General introduction

> *"Our evidence for the past, whether recent or distant, is constantly being diminished by the unremitting processes of decay and destruction. The forces of destruction and deterioration range in scale from the wholesale obliteration of landscapes [...] to the more subtle agencies of transformation and disintegration that steadily erode man's remains in the buried environment. Often the loss is so great that it seems impossible to reconstruct with confidence man's activities in the past. Despair is, however, unwarranted. [...] When the mechanisms of reduction and the decayed fragments of evidence are examined systematically a wealth of information is revealed..."*
>
> Preface of *Death, Decay, and Reconstruction: Approaches to Archaeology and Forensic Sciences* by Boddington *et al*. (1987).

## 1. HOMININ FOSSILS FROM SOUTH AFRICAN CAVE DEPOSITS

Fossil-bearing cave deposits of South Africa have produced one of the most abundant collections of early hominins and associated fauna for the Plio-Pleistocene. The caves have accumulated and preserved the bones of several different genera and species of early hominins (*Australopithecus africanus*, *Australopithecus* "second species"*, Australopithecus sediba, Paranthropus robustus*, early *Homo*, and *Homo ergaster*) and modern humans (*Homo sapiens sapiens*), contributing to enrich our general understanding of hominin evolution (Dart, 1925; Broom, 1938; Robinson, 1953, 1961; Clarke, 1985; Berger *et al*., 2010). South African cave deposits cover a period that begins in the early Pliocene (Way Point 160 at Bolt's Farm; Sénégas and Avery, 1998) to the present (de Ruiter and Berger, 2000). To date, 17 Plio-Pleistocene fossil-bearing localities from

cave deposits have undergone excavations (Bolt's Farm, Buffalo Cave, Cooper's, Drimolen, Gladysvale, Gondolin, Haasgat, Kromdraai, Luleche, Makapansgat, Malapa, Minnaars, Motsetse, Plovers Lake, Sterkfontein, Swartkrans and Taung) (Eitzman, 1958; Brain, 1981, 1993; Hendey, 1981; Keyser and Martini, 1990; Keyser, 1991; Berger *et al*., 1993; McKee and Tobias, 1994; Keyser *et al*., 2000; Berger and Lacruz, 2003; Berger *et al*., 2003; Brophy, 2004; Hilton-Barber and Berger, 2004; Adams, 2006; Adams *et al*., 2007a, 2007b; Thackeray *et al*., 2008; de Ruiter *et al*., 2009; Dirks *et al*., 2010; Gommery *et al*., 2012). Most of these cave sites are composed of several distinct layers or deposits with different genesis and ages, such as Sterkfontein (13 deposits: Members 1, 2, 3, 4, 5 "StW 53", 5 "East Infill", 5 "West Infill", 5 "Oldowan Infill", 6, Lincoln Cave North and Lincoln Cave South, Name Chamber, Silberberg Grotto and Jacovec Cavern; Brain, 1981; Kuman and Clarke, 2000; Kibii, 2004; Reynolds and Kibii, 2011), Swartkrans (six deposits: Member 1 "Lower Bank", Member 1 "Hanging Remnant", Members 2 to 5; Brain, 1981, 1993), Cooper's (three deposits: A, B and D; de Ruiter *et al*., 2009), Kromdraai (two deposits: A and B; Brain, 1981), Gondolin (three deposits: 1, 2 and A; Adams, 2006), Gladysvale (two deposits: the internal roofed section, GVID, Gladysvale Internal Deposits; and the external de-roofed section , GVED, Gladysvale External Deposits; Lacruz, 2002; Lacruz *et al*., 2002; Pickering, 2005; Pickering *et al*., 2007), Bolt's Farm (23 deposits; Thackeray *et al*., 2008), Taung (ten deposits, including five located in the "Dart deposits", D-A to D-E; and five in the "Hrdlička deposits", H-A to H-E; Peabody, 1954; McKee, 1993; McKee and Tobias, 1994), and Makapansgat (five Plio-Pleistocene deposits from the Limeworks Australopithecine site, namely Members 1A, 1B, 2, 3 and 4; and the archaeological deposits from the Cave of Hearths, Historic Cave, and Rainbow Cave; Latham *et al*., 1999; Latham and Herries, 2004). A recent campaign of prospecting in the Cradle of Humankind has revealed the presence of 96 other fossil-bearing sites yet to be excavated, including 15 sites containing hominin or archaeological remains (Dirks and Berger, 2012). The abundance of fossil hominins and associated fauna (ungulates, carnivores, rodents, microfauna, reptiles and birds) has allowed an extremely rich and diverse field of

palaeontological studies to develop. Numerous aspects of past life and landscapes can be explored (e.g. environment, habitat, ecology, behaviour, diet, biomechanics and locomotion) and numerous questions regarding the evolutionary pattern of our ancestors, such as understanding the mechanisms of speciation and extinction events, as well as their adaptation skills and responses to their changing environment, may be addressed.

## 2. TAPHONOMIC ISSUES

The preservation of such an important fossil record can be explained by the way bones accumulated in the deposits, promoted by the existence of complex sub-surface and underground dolomitic cave systems, which collected skeletons of hominins and other animals, as well as the geochemical processes associated with the dissolution and precipitation of limestone, which enhanced the preservation of the fossils. Hence, the fossil assemblages recovered in cave deposits offer snapshots of the environment and living fauna through time. However, they may literally represent snapshots of single events, or they may be the result of long term accumulation processes, which took place over hundreds or thousands of years. Because of the nature of bone accumulation within caves, the question of the representativeness of these fossil assemblages as indicative of once living ecosystems needs to be addressed. Different biological and physical agents participate in the formation of fossil deposits in caves, such as carnivores, birds of prey, rodents, hominins, flooding, collapse, and rainfall. Each of these agents accumulates and modifies bones in a selective way. Furthermore, they occur alternatively and/or in combination with one another (in other words, it is extremely seldom to find an assemblage *exclusively* accumulated by leopards for instance, or an assemblage *exclusively* accumulated by the action of water transporting bones inside a cave). Timing of bone accumulation in caves is also difficult to estimate, since these processes tend to be gradual and can take place for years rather than as a single quick event. Consequently, understanding the taphonomy of a fossil assemblage, or, as first defined by the palaeontologist Efremov, understanding the study of the transition of once living elements

from the biosphere to the lithosphere (Efremov, 1940), is a necessary prerequisite to any palaeontological analysis. Taphonomic agents have various effects on a bone assemblage and condition a lot of aspects of the assemblage itself, such as the composition of the faunal spectrum, frequencies of different body parts, type of mortality profile, spatial distribution of the remains within the deposit and modifications observed on the bones. All these elements constitute the bases of palaeoenvironment and palaeohabitat reconstructions; they also contribute to ongoing debates on past ecology and behaviour of early hominins and other taxa.

For these reasons, important research on taphonomy in South African cave deposits has been conducted and a reasonably abundant literature on the question is available (Hughes, 1954; Brain, 1973, 1975, 1976, 1981, 1993; Maguire *et al*., 1980; Pickering, 1999; de Ruiter and Berger, 2000; Pickering *et al*., 2000, 2004a, 2004b, 2004c; Kibii, 2004, 2007; Adams, 2006, Adams *et al*., 2007a, 2007b; de Ruiter *et al*., 2009; Val *et al*., submitted). Most of the existing studies follow in the footsteps of the pioneering work of C.K. Brain, who was the first to conduct detailed and complete taphonomic analyses of some of the most renowned fossil deposits from South Africa (Sterkfontein, Swartkrans and Kromdraai), all presented in his book *The Hunters or the Hunted? An Introduction to South African Cave Taphonomy,* and in previous studies (Brain, 1958, 1973, 1975, 1976).

Various hypotheses have been put forward to explain the presence of early hominin remains within cave deposits, especially for deposits containing a high proportion of hominins and other large-bodied primates. The most widely accepted explanation mentioned in the literature is based on the “carnivore-collecting hypothesis”, which was first proposed by C.K. Brain (1981) and later tested and confirmed by others (de Ruiter, 2001; Carlson and Pickering, 2003; Kibii, 2004, 2007; Pickering *et al*., 2004a, 2004b, 2004c; Clarke, 2007). According to this hypothesis, a predator occupying caves, or areas near cave entrances, and specialized in preying upon primates would have been responsible for the presence of, at least, some of the primate remains in cave deposits. Extant large

carnivores, such as leopards and hyaenids, and, to a lesser degree, extinct large carnivores, such as sabre tooth cats and hunting hyaenas, would have been primary accumulators of primate bones in caves. The carnivores would either bring back their complete or partial carcasses to the cave or, especially in the case of leopards, consume them in trees overhanging cave openings (the remaining bones would then fall inside the cave) (Brain, 1981). This could, in some cases, be combined with a "sleeping site scenario", whereby hominins and other primates using cave entrances as a sleeping refuge would be preyed upon by carnivores directly inside the cave, as has been mentioned by some authors (Brain, 1981, 1993; Pickering *et al*., 2004a; Val *et al*., submitted). The involvement of large carnivores in the accumulation of hominin and non-hominin primate bones has been proposed for most of the cave deposits containing abundant primate remains. Leopards are considered the primary accumulators of the primate remains at Swartkrans Member 1 "Hanging Remnant", Swartkrans Members 2 and 3, Sterkfontein Member 4 and Kromdraai B (Brain, 1981, 1993; de Ruiter, 2001; Carlson and Pickering, 2003; Pickering *et al*., 2004a, 2004c), while spotted hyaenas have contributed to accumulate some primate bones at Swartkrans Member 1 "Hanging Remnant", Sterkfontein Member 4, Swartkrans Member 3 and Kromdraai A (Brain, 1973, 1981; Carlson and Pickering, 2003; Pickering *et al*., 2004a, 2004c). These assemblages are characterised by fragmentary and carnivore-damaged primate remains (i.e. presence of carnivore tooth marks and digested bones, and breakage patterns associated with carnivore action) and, in some cases, by specific skeletal part representation amongst the primate remains, consistent with carnivore accumulation (Carlson and Pickering, 2003; Pickering and Carlson, 2004).

A natural death trap scenario is another taphonomic hypothesis mentioned in the literature. In this case, animals, including primates, would have fallen or climbed inside the cave without been able to exit. However, concerning hominin-bearing deposits, this scenario has been proposed as the main accumulation process in *one* case only: at Sterkfontein Member 2, to explain the origin of the fossil assemblage associated with StW 573, a near-complete skeleton of an australopithecine ("Little Foot") (Clarke, 1998, 1999;

2007; Pickering *et al*., 2004a). This assemblage has specific characteristics such as the abundance in the faunal spectrum of animals with good climbing proclivities (primates and carnivores), the presence of antimeric sets of bones and partial skeletons, and the very low impact of carnivore damage on the bones (Pickering *et al*., 2004a; Clarke, 2007).

## 3. RESEARCH QUESTIONS FOR THE MALAPA ASSEMBLAGE AND OBJECTIVES OF THIS STUDY

The Malapa hominin assemblage represents a very peculiar case within the context of Plio-Pleistocene South African cave deposits, and therefore offers challenging new questions regarding early hominin taphonomy. The hominins recovered at Malapa not only represent a completely new species, *Australopithecus sediba* (Berger *et al*., 2010), combining primitive and derived characters, which places the species in a crucial position for the understanding of the emergence of the genus *Homo* (Berger *et al*., 2010; Carlson *et al*., 2011; Kibii *et al*., 2010; Zipfel *et al*., 2011; Berger, 2012), but the taphonomy of the fossils is also remarkable. The exceptional quality and abundance of bone preserved for the Malapa hominins has never been observed in any of the fossil sites in South Africa, and as such places the Malapa assemblage in a class of its own relative to the other fossil assemblages from the Cradle of Humankind. The assemblage is composed of a high number of hominin bones (*n.* >256), belonging to a minimum of six individuals, amongst which two are nearly complete (Malapa Hominin 1 - MH1 -, a juvenile male and Malapa Hominin 2 - MH2 -, an adult female). These two individuals are represented by many complete and near complete bones, in an excellent state of preservation (i.e. bone surface perfectly preserved). Some elements are still in articulation and most of the body parts have been recovered, including very small elements, such as hand and foot bones. Furthermore, the sedimentary unit (Facies D) containing the hominins has been dated accurately to 1.977-1.8 Ma (Pickering *et al*., 2011), offering one of the most precise ages for a cave deposit yielding early hominins in the Cradle of Humankind. In terms of preservation, the hominin assemblage at Malapa does not resemble any of other cave

deposits with early hominin assemblages, with the possible exception of Member 2 at Sterkfontein. It therefore challenges previous interpretations of hominin accumulation, such as the "carnivore-collecting hypothesis" and the natural death trap scenario. The specific taphonomic signatures observed at Malapa motivate for the need to question the origin of at least some hominin bones in caves and suggest that a different taphonomic scenario or, rather, a different combination of taphonomic processes, unobserved to date, may be present at Malapa. Based on preliminary observations and study of geological features of the deposit, a first hypothesis was proposed to explain the accumulation of the hominin remains at Malapa (Dirks *et al*., 2010). This hypothesis (Figure 1.1) focuses on the taphonomy of the two near-complete skeletons (MH1 and MH2):

*"As a taphonomic hypothesis, we suggest that at the time of burial of the hominins, the complex cave system near Malapa had opened along deep vertical shafts that operated as death traps to animals on the surface. In addition to being inconspicuous drops into which animals accidentally wandered, the cave openings may have been loci of animal activity, enhancing their operation as natural traps. Animals might have been attracted to the smell of water coming from the shaft, and carnivores might have been attracted to the smell of decomposing bodies. These factors could have operated to accumulate a diverse assemblage of carcasses in the chamber below, away from carnivore activity. The sediments imply that subsequent high-volume water inflow, perhaps the result of a large storm, caused a debris flow that carried the still partially articulated bodies deeper into the cave, to deposit them along a subterranean stream"* (Dirks *et al*., 2010, p.207; Figure 1.1).

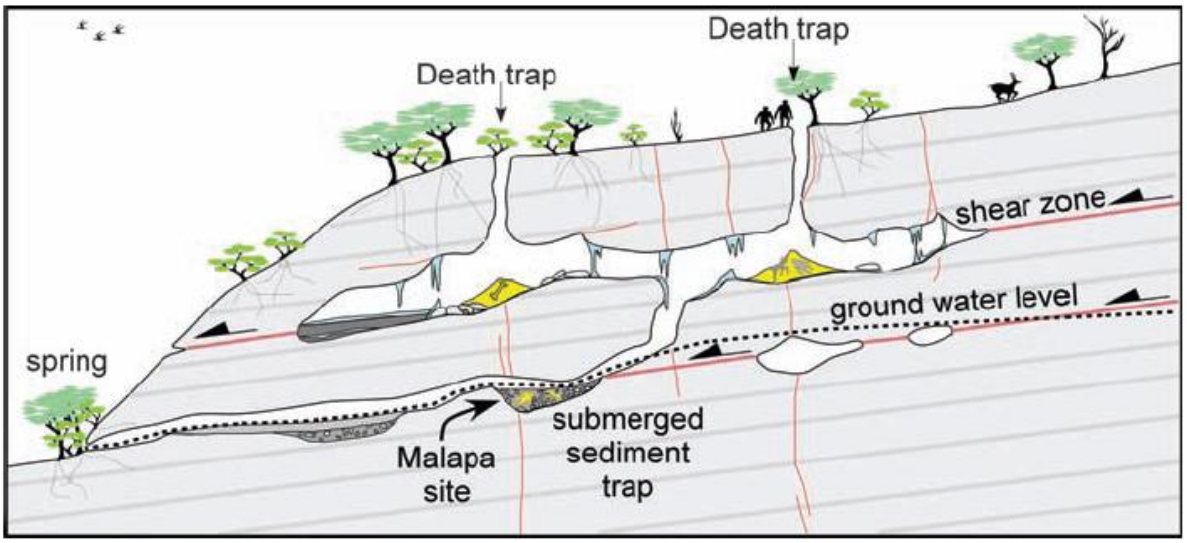



**Figure 1.1.** Cartoon illustrating the proposed hypothesis for the mode of accumulation of MH1 and MH2 (after Dirks *et al*., 2010).

Different elements, essential for the accumulation of the hominins, are proposed in this hypothesis, notably the absence of *post-mortem* carnivore modification and the effect of a debris flow happening shortly after the death of the hominins inside the cave. The hypothesis of a single event, or catastrophic accumulation, happening in a short period of time, rather than a slow attritional process, has been mentioned elsewhere to explain the high degree of preservation of the fossils (Berger, 2012). These hypotheses were proposed at an early stage of study. Since then, more hominin remains belonging to MH1 and MH2 have been prepared and recovered, together with fossils belonging to other hominin (MH3, MH4, MH5 and MH6) and non-hominin individuals. A complete, detailed analysis of the fossil assemblage is required to test and verify certain aspects of the preliminary hypothesis, such as the near absence of carnivore damage, and the role played by the debris flow. The question of the homogeneity of the hominin assemblage, as well as of the whole faunal assemblage, also needs to be addressed.

The Malapa faunal assemblage contains a high number of hominin fossils that would, *a priori*, suggest that one of the most commonly occuring scenarios (natural death trap or carnivore-collected assemblage) could be proposed as a logical explanation for

their presence in the deposit. On the one hand, the relatively good state of preservation observed for the Malapa hominins (e.g. partially articulated skeletons, antimeric sets of bones, presence of complete bones and extremely well-preserved bone surfaces), seems to be in favour of a natural death trap hypothesis. The remarkable state of preservation of the hominins is combined with the near (or perhaps even total) absence of carnivore damage, which is consistent with the very limited or non-participation by carnivores in the formation of the assemblage. Hence, the carnivore collecting hypothesis does not seem to be pertinent to Malapa. However, several observations are in contradiction with a straightforward application of the natural death trap hypothesis: (1) such a high number of hominin individuals has not been previously recorded in an assemblage that is known to have accumulated through a natural death trap; (2), in the case of a proven natural death trap scenario, all primates, including hominins and non-hominins are abundant, while at Malapa the ratio hominin to non-hominin primates is completely disproportionate (256 hominin specimens have been recovered and only one non-hominin primate specimen).

The aim of this PhD is to test the validity of the preliminary taphonomic hypothesis (i.e. natural death trap followed by a debris flow leading to a rapid burial of the hominins) and provide further insights into the different taphonomic processes that have contributed to the accumulation of the Malapa hominin bones. This requires a more detailed understanding of the formation of the faunal assemblage that has been recovered to date.

Testing taphonomic hypotheses is not always easy because it relies on the methods employed and information recorded during the excavation, preparation and analysis of the fossil remains. The majority of South African fossil-bearing caves have been discovered through mining, leading to the destruction of some fossils and to the loss of spatial and stratigraphic information. Hence, fossils from many sites were recovered from *ex situ* blocks of calcified clastic sediment. In the case of fossils recovered *in situ* during

earlier excavations, the record of the coordinates was not always systematic and in most cases the provenance, position, and orientation of the remains in the deposit are not known. A complete taphonomic analysis of a fossil faunal assemblage should ideally be based on the combination of three different approaches in order to collect as much evidence as possible to understand the full depositional history. The two classical ones commonly used in taphonomy are: a palaeontological approach (study of the faunal spectrum composition, estimation and interpretation of skeletal part representation and mortality profiles) and a physical approach (analysis of bone surface modifications and identification of the modifying agents) (see Domínguez-Rodrigo *et al*., 2007). A third approach, the spatial approach, has been underused in the field of taphonomy of cave deposits given the lack of useful information, as mentioned above, (i.e. no record of the coordinates, no data about the position and orientation of the fossils when found *in situ*, and fossils recovered from *ex situ* blocks). In more recently excavated cave sites, the use of a laser theodolite allows for the systematic and accurate recording of the coordinates and, in the future, more spatial studies should be conducted. So far, only one spatial study of a Plio-Pleistocene cave deposit in South Africa has been published (Nigro *et al*., 2003), which developed and applied a Geographical Information System (GIS) for mapping and analysing the distribution pattern of the fossils at Swartkrans.

At Malapa, while some remains were recovered from *ex situ* blocks, others have been recovered *in situ*. All the specimens have been given coordinates, and in some cases, the position and orientation of the fossils in the deposit is known, preventing the loss of any spatial information. In this research project, I employed virtual techniques, namely Computed Tomography (CT) and micro-CT scanning facilities as well as 3D rendering software (Avizo 6.3) to conduct a spatial analysis of the *in situ* fossils inside the cave. Scanning and 3D reconstruction techniques are nowadays frequently used in different fields of palaeoanthropology, such as morphometry, biomechanics, study of bone density, reconstruction of distorted fossils and virtual exploration of fragile fossils and/or inaccessible parts of the fossils (Conroy and Vannier, 1984; Wind, 1984; Luo and Ketten,

1991; Zollikofer *et al*., 1998, 2002, 2005; Maisey, 2001; Carlson and Pickering, 2003; Novecosky and Popkin, 2005; Zollikofer and Marcia Ponce de León, 2005; Lordkipanidze *et al*., 2006; Carlson *et al*., 2011; Val *et al*., 2011; Guyomarc'h *et al*., 2012; Colombo *et al*., 2012). However, these techniques have never been applied to address taphonomic questions.

At Malapa, the spatial analysis of the hominin remains aims to reconstruct the burial position of MH1 and MH2 inside the deposit, in three dimensions. Until now, there has been no attempt to reconstruct and analyse the burial posture of an early hominin. Analysing burial posture for early hominin fossils is exceedingly difficult, given their typical preservation in cave deposits or open air contexts, where they are vulnerable to a plethora of destructive taphonomic agents and processes. These processes commonly transform the skeletons into fragmented, parautochtonous remains.

On the other hand, in palaeontological (e.g. Smith, 1987, 1993, 1995; Weigelt, 1989; Ochev, 1995; Smith and Evans, 1996; Smith and Ward, 2001; Damiani *et al*., 2003; Adbala *et al*., 2006; Botha-Brink and Modesto, 2007; Faux and Padian, 2007; Stanford *et al*., 2011; Fordyce *et al*., 2012), archaeological (e.g. Binford, 1968; Harrold, 1980; Gargett, 1989, 1999; Koojmans *et al*., 1989; Smirnov, 1989; Belfer-Cohen and Hovers, 2002; Kimbel *et al*., 1995; Duday, 2009) and modern historical sites (e.g. Mastrolorenzo *et al*., 2001, 2010; Roksandic, 2002; Luongo *et al*., 2003; Duday, 2009), the burial posture of vertebrate skeletons, including humans, when complete or near complete and found *in situ*, is generally described and studied. It can provide a wealth of information about the timing and the conditions of burial, and, in the case of modern funeral contexts, about the mortuary behaviours of past populations. When complete burial happens simultaneously or soon after death, the death pose can be preserved, and provides direct information about the site of death, the factors that influenced death, as well as factors that have an impact on preservation. At Malapa, the high level of preservation of the hominins and the existence of accurate information regarding the origin of the fossils in the deposit,

combined with the application of virtual reconstruction techniques, allow for the first time the reconstruction and analysis of the burial position of the two hominins (MH1 and MH2). This research will (1) provide information about the mode and timing of burial of the hominins, and the conditions under which it took place, (2) allow an estimation of the state of decay and disarticuation of the hominins when burial occurred, and therefore permit an evaluation of the chances of survival of soft tissue, and (3) open the possibility to put forward hypotheses regarding the location of missing elements inside the deposit.

To summarize, this project is the first of its kind to combine three research approaches: palaeontological, physical and spatial, and to apply modern investigation methods, such as CT-scanning and 3D modelling techniques to address taphonomic questions about early hominins. The taphonomy of the hominins is approached and analysed as a forensic case, combining all available types of evidence to precisely reconstruct the conditions and timing of burial of MH1 and MH2. The Malapa hominin assemblage is used as a case study, remarkable for its various characteristics in terms of bone preservation. Ultimately, this research aims specifically to increase our understanding of the formation of the fossil assemblage at Malapa, and more generally to expand our knowledge of the processes of bone accumulation, modification and preservation in caves. From a research perspective it seeks to develop a new multidisciplinary approach to better understand the taphonomy of hominin remains, combining classical taphonomical methods with virtual techniques and modern forensic methods of investigation.

## 4. THESIS OUTLINE

A general literature review of the state of knowledge regarding hominin taphonomy in South African caves and fluvial contexts (palaeoriverine and palaeolake deposits from Central and Eastern Africa) is presented in Chapter 2. The fossil material analysed for this research project (hominin as well as non-hominin faunal specimens) is described in Chapter 3. The different methods employed to investigate the taphonomy of the

assemblage are explained in Chapter 4. The three types of approaches followed, namely palaeontological, physical and spatial, together with the corresponding methods used, especially the CT scanning and virtual reconstruction techniques are described. The concept of "*palaeoforensic taphonomy"* is proposed as research practice. The Malapa fossil locality is presented in Chapter 5, including geographical, geomorphological and geological aspects of the site, as well as preliminary hypotheses for the taphonomy history of the hominins. A general description of the available faunal assemblage associated with the hominins is included in this chapter and comprises information regarding the composition of the faunal spectrum in terms of species and body parts, the state of preservation and articulation of the faunal remains, as well as the types of bone surface modifications observed. Chapter 6 presents the results of a detailed taphonomic analysis of the hominin remains, and the results of the palaeontological and physical approaches. The skeletal part survival, state of articulation of MH1 and MH2, the level of completeness, breakage patterns and bone surface modifications, together with the identification of the agents responsible, are assembled in this chapter. Chapter 7 presents the results of the spatial approach, including the origin of the hominin remains in the deposit, estimation of the transport and movement affecting the fossil remains, refitting hypotheses for the *ex situ* hominin specimens in the deposit, and creation of the 3D reconstruction model presenting the hominins in their burial posture in the deposit. Chapter 8 integrates the results into a comprehensive reconstruction of the taphonomic history of the hominins. A step-by-step account of the sequence of events that affected the hominins is described, including the mode of entry into the site, configuration of the site at the time of death, nature and timing of decay and disarticulation, conditions of transportation, context and modalities of burial. Various questions are addressed, such as the possibility of natural mummification, the role played by insects, and the occurrence and effects of a debris flow. The implications of the results and the research perspectives offered by this thesis are presented in Chapter 9. Different hypotheses concerning the location of some missing hominin remains and the reassignement of some hominin

specimens are proposed. There is discussion about the advantages offered by the virtual reconstruction techniques and the forensic approach. In conclusion, reflections on this research are made and advice about future excavations is offered.

# Chapter 2. Early hominin taphonomy from African deposits

A unifying feature of modern humans is their fascination with their ancient past. While societies all over the globe have developed creation myths to explain the origination of our species, the scientific evidence points to Africa as the origin site for early hominins. Only three small regions in Africa preserve the remains of early humans and their ancestors, namely hominins: Eastern, Central and Southern Africa, with a slim corridor of remains in between. Eastern and Central African fossils are typically in sediments deposited along ancient lake margins or river floodplains, while South African hominin remains are typically preserved in dolomitic cave systems. This chapter explores how and why early hominins are recorded in a handful of caves in an area of South Africa known as the Cradle of Humankind, as well as in the palaeolake and palaeoriver deposits of Central Africa and along the Rift Valley in East Africa.

## 1. HOMININ TAPHONOMY IN CAVE DEPOSITS OF SOUTH AFRICA

### 1.1. Presentation of the region

#### *1.1.1. Fossil-bearing sites in the Cradle of Humankind*

The Cradle of Humankind World Heritage Site is composed of 15 excavated fossil localities (Bolt's Farm, Buffalo Cave, Cooper's, Drimolen, Gladysvale, Gondolin, Haasgat, Kromdraai, Luleche , Malapa, Minnaars, Motsetse, Plovers Lake, Sterkfontein, and Swartkrans; Figure 2.1), distributed in two provinces. The majority of them are located in the Gauteng Province (Bolt's Farm, Buffalo Cave, Cooper's, Drimolen, Gladysvale, Kromdraai, Malapa, Minnaars, Motsetse, Plovers Lake, Sterkfontein and Swartkrans) and three of them are north of this region, in the Northwest Province (Gondolin, Haasgat, and Luleche). The oldest deposit in the Cradle is probably Way Point 160 at Bolt's Farm, where biochronological dating based on the microfauna provided an age between 4.0 to 4.5 Ma years (Sénégas and Avery, 1998). The cave sites of the Cradle occur in the dolomitic rocks

of the Transvaal Supergroup, which formed 2.6 to 2.8 billion years ago (Eriksson and Truswell, 1974; Martin *et al*., 1998).

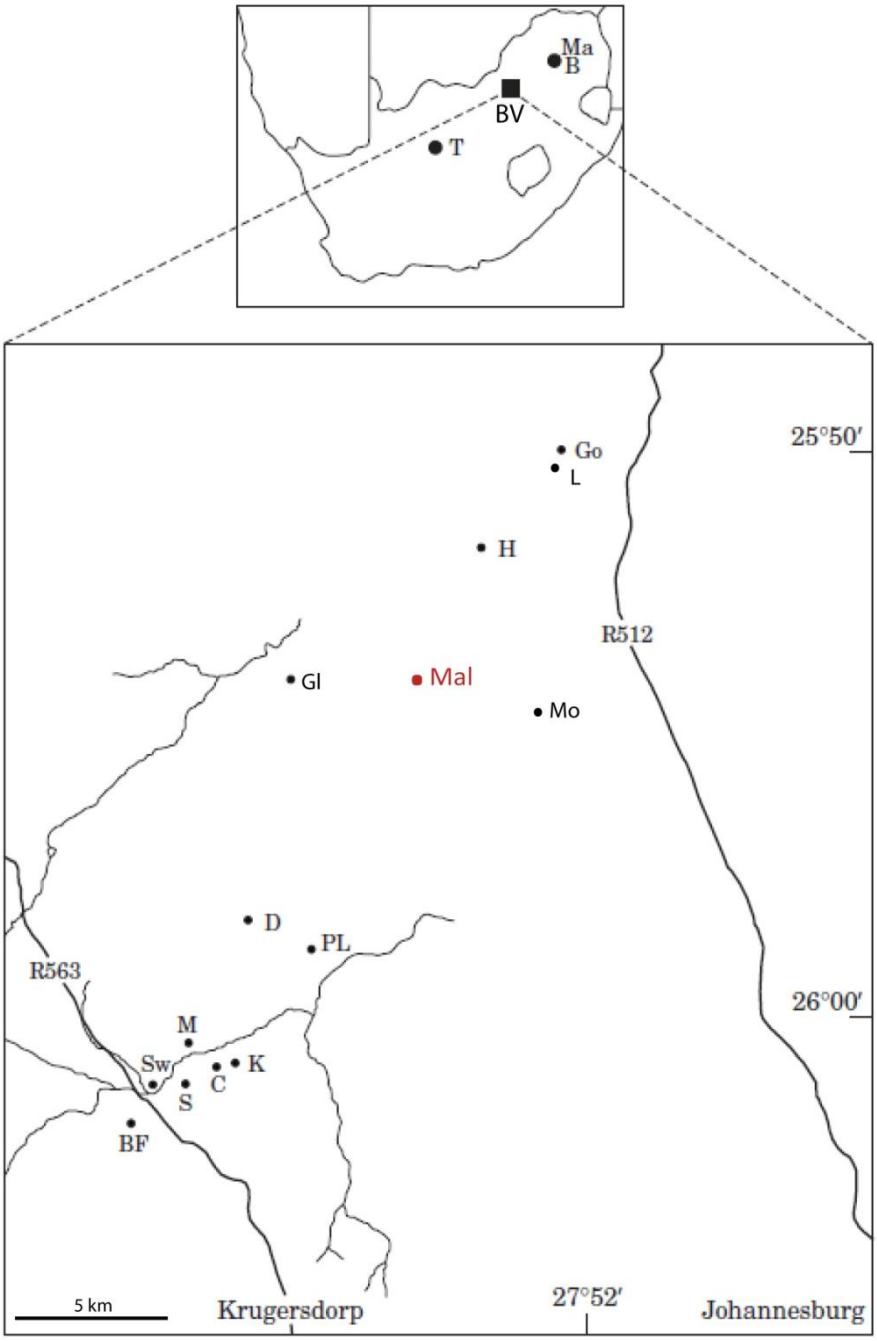



**Figure 2.1.** Location of important fossil deposits in South Africa, including localities in the Cradle of Humankind (CoH): Bolt's Farm (BF), Cooper's (C), Drimolen (D), Gladysvale (Gl), Gondolin (Go), Haasgat (H), Luleche (L), Kromdraai (K), Minnaars (M), Malapa (Mal), Motsetse (Mo), Plovers Lake (PL), Sterkfontein (S), Swartkrans (Sw); and outsite of it: Buffalo Cave (B), Makapansgat (Ma), and Taung (T) (modified after Kuman and Clarke, 2000; Berger and Lacruz, 2003; Adams *et al*., 2007b; Dirks and Berger, 2012).

The majority of the sites were subjected to limestone mining from the late 19th century to the middle of the 20th century, which exposed the fossil-rich breccias (Brain, 1981; Wilkinson, 1983; Hilton Barber and Berger, 2002; Pickering, 2005; Adams, 2006).

*1.1.2. Hominin discoveries*

Amongst the different fossil localities known in the Cradle of Humankind, eight of them (i.e. Sterkfontein, Swartkrans, Kromdraai B, Cooper's D, Gladysvale, Gondolin A, Drimolen, and Malapa) have yielded hominin remains in Gauteng Province, attributed to at least seven species (Table 2.1). Outside of the Cradle of Humankind, hominin remains have also been recovered in Taung in the Northwest Province and in Makapansgat in Limpopo Province (Dart, 1925, 1948a). The first early hominin was identified by Dart in 1925 at Taung. The skull of a child discovered in the deposit was described as the holotype of a new species, namely *Australopithecus africanus* (Dart, 1925). In 1936, Broom identified the first hominin specimen at Sterkfontein, from Member 4. The adult hominin specimen (a fragmentary skull) was first named *Plesianthropus transvaalensis*, and was later subsumed into the species *africanus* (Broom, 1936, 1947; Brain, 1981). Another species, *Australopithecus prometheus*, was identified at Makapansgat (Dart, 1948a, 1948b, 1949) and later subsumed into *africanus* as well (Clarke, 2008). Clarke (1985, 1986, 1988) has argued in favour of the attribution of some hominin remains found in Sterkfontein to a different australopithecine species. This other species has to date not been given a taxonomic name and is referred as *Australopithecus* "second species" (Clarke, 1985, 1986, 1988). The near-complete skeleton of StW 573 (nicknamed "Little Foot") discovered in the Silberberg Grotto (Sterkfontein Member 2) has been attributed to this "second species" (Clarke, 2008). The remains of two nearly complete skeletons belonging to a gracile australopithecine species were discovered at Malapa in 2008 by Berger and attributed to a new species, *Australopithecus sediba* (Berger *et al*., 2010; Table 2.1).

**Table 2.1**. Age ranges of the different hominin taxa identified in the Cradle of Humankind and Taung, together with the localities where they were found.

| Taxon | First appearance | Last appearance | Fossil sites | References |
|---|---|---|---|---|
| ***Au. africanus*** | 2.8/2.6 Ma | 0.6 Ma | Taung, Sterkfontein Member 4; Gladysvale | Dart, 1925; Broom, 1936, 1947; Berger *et al*., 1993; Berger and Tobias, 1994; Lacruz *et al.*, 2002 |
| ***A. "second species"*** | 3.3 Ma | 2.0 Ma | Sterkfontein Member 4 and Member 2 of the Silberberg Grotto ("Little Foot") | Clarke, 1988, 1998, 1999, 2008 |
| ***P. robustus*** | 2.0 Ma | 1.0-0.6 Ma | Kromdraai B; Swartkrans Members 1-3, Drimolen, Sterkfontein Member 5 (East infill); Coopers' D; Gondolin A | Broom, 1938 ; Brain, 1981, 1993; Grine, 1993; Berger and Tobias, 1994; Menter *et al.*, 1999 ; Keyser, 2000 ; Keyser *et al*., 2000 ; Kuman and Clarke, 2000; Berger *et al*., 2003; de Ruiter *et al*., 2009 ; Herries *et al*., 2009 |
| ***Au. sediba*** | 1.977 Ma | 1.977 Ma | Malapa | Berger *et al*., 2010 ; Dirks *et al*., 2010 ; Pickering *et al*., 2011 |
| ***early Homo*** | ~2.0 Ma | 1.0-0.6 Ma | Sterkfontein StW 53 infill, Swartkrans Members 1-2, Drimolen, Kromdraai B | Hughes and Tobias, 1977; Brain, 1981, 1993; Grine, 1989, 1993, 2005; Keyser, 2000; Keyser *et al*., 2000; Braga and Thackeray, 2003; Herries *et al*., 2009 |
| ***H. ergaster*** | 1.7-1.4 Ma | 253-115 ky | Sterkfontein (Member 5 West infill and Lincoln Cave South) | Kuman and Clarke, 2000; Reynolds *et al*., 2003, 2007 |
| ***H. sapiens*** | 0.5-0.3 Ma | - | Sterkfontein Post-Member 6; Swartkrans Member 5 | Watson, 1993; Kuman and Clarke, 2000; Herries and Shaw, 2011 |

A more robust taxon, *Paranthropus/Australopithecus robustus*, was identified for the first time by Broom at Kromdraai B in 1938 (Broom, 1938) and the remains of this species were subsequently recovered in various other sites of the Sterkfontein Valley (Table 2.1).In 1953, Robinson identified, for the first time, remains of early *Homo* at Swartkrans (firstly classified as *Telanthropus capensis* and then attributed to the genus *Homo*; Robinson, 1953, 1961). Shortly thereafter, in 1976, the remains of *Homo habilis* were recovered at Sterkfontein Member 5 by Hughes (specimen StW 53) and described by various authors (Hughes and Tobias, 1977; Brain, 1981; Robinson, 1953, 1961; Clarke, 2012). The assignement of these remains to the genus *Homo* is not accepted by some workers and is currently under discussion (see for instance Curnoe and Tobias, 2006; Curnoe, 2010; Pickering *et al*., 2011; Berger, 2012). Specimens of *Homo ergaster* have been found during the course of excavations in the Sterkfontein Member 5 East infill and Lincoln Cave (Reynolds *et al*., 2003; Reynolds and Kibii, 2011; Clarke, 2012). Finally, remains of modern humans were recovered at Sterkfontein Post Member 6 (Kuman and Clarke, 2000; Reynolds and Kibii, 2011) and Swartkrans Member 5 (Watson, 1993).

## 1.2. Hominin taphonomy

### *1.2.1. Introduction*

More than a thousand early hominin specimens have been recovered in the different cave deposits of the Cradle of Humankind (Hilton Barber and Berger, 2002). The state of preservation of these remains is highly variable, from near complete skeletons such as “Little Foot” at Sterkfontein and the two individuals from Malapa, to bone and tooth fragments. Some sites have yielded hundreds of specimens whereas others have produced only a handful. The extreme variability between deposits from the same period and the same region can partly find an explanation in the variability of bone accumulating agents, taphonomic and site formation processes active in the dolomitic caves as well as patterns of exploration and excavation.

*1.2.2. Geomorphology and formation of the fossil deposits in dolomitic caves*

Brain (1958, 1981) has defined a 6-stage process to explain the formation of the fossil-bearing cave deposits in the dolomitic region of the Cradle of Humankind. In the first stage, a cavity forms in the dolomite due to the action of underground water in the phreatic zone dissolving the rock. As the watertable drop this cavity enlarges and is then filled with air (stage 2). Some speleothems can appear and avens start forming in the dolomite roof above the cavern (stage 3) until the cavern eventually opens to the surface to form a cave, which is then progressively filled with sediments, rocks and bones (stage 4) that accumulate on a talus cone. This talus cone is commonly calcified due to lime-bearing solutions dripping from the roof and becomes "calcified clastic sediment" or so-called "breccias" (stage 5). In stage 6, the roof is eroded and the calcified clastic sediment is exposed to surface weathering (Brain, 1981).

The first type of taphonomic agents leading to bone accumulation in caves are abiotic, such as gravity, flood, wind/rain washing carcasses, bones and bone fragments from the surface into the cave (Maguire *et al*., 1980; Brain, 1981; Texier, 2000). Included in this category is animal death, whether naturally occurring by inhabitants of caves, or unintentionally, from falling into death trap situations. The second category of taphonomic agents leading to bone accumulation are biotic agents that occupy the caves and their surroundings (e.g. overhanging trees, roofs) and accumulate bones. Predators and scavengers introduce animal bones to their lairs in caves while feeding, defecating, and/or regurgitating (Sutcliffe, 1970; Mills and Mills, 1977; Maguire *et al*., 1980; Binford, 1981; Brain, 1981; Skinner and van Aarde, 1991; Berger and Tobias, 1994; de Ruiter and Berger, 2000, Lacruz and Maude, 2005; Berger, 2006; Kuhn, 2006). Rodents, such as porcupines, collect bones in their cave dens in order to gnaw on them to wear down their incisors (Maguire *et al*., 1980; Binford, 1981; Brain, 1981; Kibii, 2009).

Early hominins and other large-bodied primates are accumulated in cave deposits by similar agents, whether by predators or through a natural death scenario. Hominin and

non-hominin primate taphonomy will be discussed together below, before considering the case of cave occupation and use by hominins, which differs from other primates. A brief review is given of which, and how, different taphonomic agents have contributed to the accumulation of early hominin bones in southern African dolomitic caves.

### *1.2.3. Primate bones in cave deposits: causes of accumulation*

#### Abiotic agents: debris flow, rain and gravity

The action of rain, wind and gravity contributes to the formation of a talus cone below cave roof openings (Brain, 1981; Texier, 2000; Adams *et al*., 2007a), containing not only bones and bone fragments but also anything that is on the surface near the opening (e.g. rocks, artefacts, leaves, tree trunks, and fine sediments). This process has contributed to a greater or lesser degree to bone accumulation in all the cave deposits from the Cradle of Humankind, including fragmentary hominin bones (Brain, 1981). The state of fragmentation and the stage of weathering of bone fragments can be a good indicator of the time of exposure on the surface before the bones were finally and completely buried in the cave deposit (Miller, 1975; Behrensmeyer, 1978).

#### Falling accidents

Natural openings in the rooftop of caves are usually surrounded by clusters of trees, since trees thrive in the presence of underground water. This would make their visibility poor and it is therefore not surprising that larger animals walking on the surface could easily fall into them by accident (Brain, 1981). Some of these shafts or "natural death traps" were several tens of metres high during the Plio-Pleistocene (Brain, 1975, 1981; de Ruiter *et al*., 2009; Dirks *et al*., 2010; Pickering *et al*., 2011). Some species with good climbing proclivities such as primates and carnivores could also have deliberately entered the caves along these steep openings and in some cases found it impossible to return to the surface. A natural death trap scenario has been invoked to explain the bone accumulation process in Sterkfontein Member 2, including the remains of StW 573 or

"Little Foot" (Pickering *et al*., 2004a; Clarke, 2007), as well as to explain the presence of numerous articulated elements in the Kromdraai A faunal assemblage (Brain, 1973, 1981). The preservation of articulated elements and antimeric sets of bones, good representation of the different skeletal parts, and the absence of carnivore and rodent damage, are considered as good indicators of a natural death trap scenario (Costamagno, 1999; Pickering *et al*., 2004a; Clarke, 2007; Coumont, 2009).

Biotic agents: mammalian carnivores

*Primate bone assemblages and the "carnivore-collecting hypothesis"*

Large carnivores, and especially leopards and hyaenas, have contributed to the accumulation of faunal assemblages in the different fossil sites from the Cradle of Humankind (Table 2.2).

**Table 2.2**. Accumulating carnivore agents proposed for the primate remains in some cave sites from the Cradle of Humankind.

| Cave deposit | Member | Origin of the primate remains | References |
|---|---|---|---|
| **Sterkfontein** | 4 | leopard & hyaena | Brain, 1981; Pickering *et al*., 2004b |
| **Swartkrans** | 1 (Hanging Remnant) | leopard & hyaena | Brain, 1981, 1993; de Ruiter, 2001; Carlson and Pickering, 2003 |
| | 2 | leopard | Brain, 1981, 1993; Carlson and Pickering, 2003 |
| | 3 | leopard & hyaena | Brain, 1981, 1993; Pickering *et al*., 2004c |
| **Kromdraai** | A | hyaena | Brain, 1973, 1981 |
| | B | leopard | Brain, 1981 |

To explain the abundance of primate remains in some of the assemblages, Brain has elaborated the "carnivore-collecting hypothesis" (Brain, 1981), whereby a predator specialized in preying upon primates, such as leopards and to a lesser degree hyaenas, would have contributed greatly to the accumulation of primate bones. Several taphonomic studies of fossil localities in the Cradle of Humankind have confirmed the preponderant role of felids and hyaenids in the formation of primate assemblages. Hence, their impact has been identified in the accumulation of the primate remains at Swartkrans

Member 1 Hanging Remnant, Members 2 and 3, Sterkfontein Member 4, and Kromdraai A and B (de Ruiter, 2001; Carlson and Pickering, 2003; Pickering *et al*., 2004b, 2004c; Clarke, 2007; Kibii, 2007) (Table 2.2).

*Processes of bone accumulation/modification by large carnivores in cave deposits*

Two types of accumulation of carnivore-damaged bones in caves are recognised. The first type is consistent with primary deposition of bones within the cave as a consequence of carnivores bringing carcasses inside. Some species of carnivores occupy caves for various purposes such as breeding dens, places to store food and retreat for shelter (Kruuk, 1972; Brain, 1981; de Ruiter and Berger, 2000; Skinner and Chimimba, 2005; Kuhn, 2006). They can consequently introduce carcasses or elements of carcasses to feed on and/or feed their offspring inside the cave. The second type is a secondary accumulation, whereby the bones remaining after a carnivore has fed on them, are brought inside the cave through another biotic or abiotic process (e.g. collected by porcupines, washed inside the cave, accumulated by natural gravity). This happens in the case of leopards in particular, when bones fall from the tree where the predator stores a carcass. To avoid competition with other carnivores, leopards stash and eat their prey in trees, and since trees commonly grow above cave openings, the remainder of the carcass commonly falls down into the cave and contributes to the formation of the talus cone (Simons, 1966; Sutcliffe, 1973; Brain, 1981; de Ruiter and Berger, 2000; Skinner and Chimimba, 2005).

It is important to distinguish between these two modes of accumulation since they correspond to two clearly different patterns, especially when we need to distinguish between carnivore and human occupation of a site. In other words, the occurrence of carnivore chewing marks on bone specimens does not necessarily mean that carnivores have occupied the site. It could simply reflect bone fragments bearing tooth marks coming from the surface and brought into the caves by another process. Therefore, the consideration of different lines of evidence is required to distinguish between carnivore occupation of the site and falling in or washing in of carnivore-modified bones. This

evidence concerns not only carnivore tooth-mark abundance, but also the faunal composition, skeletal part representation, mortality profiles, breakage pattern of long bones and the occurrence of other indicators, such as digested bones, carnivore deciduous teeth, and coprolites (Brain, 1981; Pickering, 1999, 2002; Kuhn *et al*. 2010).

*Felids*

Extant leopards (*Panthera pardus*) are considered the primary accumulators of primates in caves of Southern African regions (Brain, 1968, 1969, 1981, 1993). The arguments for this theory are the following: (1) modern leopards include primates in their diet, (2) they frequently use caves in the southern African regions, (3) they have the habit of eating their prey in trees overhanging the dolomitic cave openings (Simons, 1966; Sutcliffe, 1973; Brain, 1981, 1993; de Ruiter and Berger, 2000; Skinner and Chimimba, 2005), and (4) fossil bones of leopards are recovered in the faunal assemblages (Brain, 1968, 1969, 1981; Watson, 1993; Reynolds, 2010). There is no record in the literature of other extant medium or large-sized felid species (i.e. *Acinonyx jubatus* and *Panthera leo*) transporting skeletal elements far from the kill site (Shaller, 1972). These species are also not known to occupy nor accumulate bones within caves (Skinner and Chimimba, 2005). Extinct large felids such as the false sabre-tooth cats (*Dinofelis barlowi* and *Dinofelis piveteaui*) and the true sabre-tooth cats (*Megantereon barlowi, Megantereon cultridens* and *Homotherium latidens*) are present in the Plio-Pleistocene fossil assemblages of the Sterkfontein Valley (Brain, 1981; Turner, 1987a, 1987b, 1997, 2004; Cooke, 1991; Watson, 1993; de Ruiter, 2003; Kibii, 2004; Pickering *et al*., 2004a; Lacruz *et al*., 2006; Hartstone-Rose *et al*., 2007; Gommery *et al*., 2008, 2012; de Ruiter *et al*., 2009; Reynolds, 2010; Kuhn *et al*., 2011) (Table 2.3). These extinct felid species would have competed with leopards and hyaenids for the same prey (O'Regan and Reynolds, 2009). Using as the main argument the abundance of extinct sabre-tooth cat remains in the Plio-Pleistocene cave deposits of the Sterkfontein Valley, Brain (1981) has suggested that these taxa could have frequently occupied caves and would have therefore been important bone collecting

agents. However, there is to date no mention in the literature concerning bone-collecting behaviour by *Megantereon* or *Dinofelis* (Pickering, 1999; Pickering *et al*., 2004b; Lacruz *et al*., 2006; Hartstone-Rose *et al*., 2007; Reynolds, 2010). There is only one published example of cave occupation by an extinct species of large felid: the late Pleistocene Friesenhahn Cave (Texas, USA), where the American subspecies *Homotherium serum* is regarded as the main agent in the accumulation of the juvenile mammoth bones within the deposit (Marean and Ehrhardt, 1995). Different arguments have been proposed to defend the theory of cave use by this carnivore as a breeding den and feeding retreat: the abundance of *Homotherium* remains within the assemblage (most abundant carnivore and second most abundant large mammal), the occurrence of articulated juvenile *Homotherium* individuals, the catastrophic mortality profile amongst *Homotheriums* and the abundance of juvenile mammoth remains, interpreted as an evidence of specialized-hunting by *Homotherium* (Marean and Ehrhardt, 1995).

*Hyaenids*

The two southern African extant hyaenid species (*Crocuta crocuta*, the spotted hyaena and *Parahyaena brunnea*, the brown hyaena) occupy caves and collect bones (Kruuk, 1972; Mills and Mills, 1977; Maguire *et al*., 1980; Binford, 1981; Brain, 1981; Hill, 1989; Skinner and van Aarde, 1991; Lam, 1992; Lacruz and Maude, 2005; Kuhn, 2006). By extension, it has been proposed that the extinct long legged hunting hyaenas (*Chasmaporthetes nitidula* and *Chasmaporthetes silberbergi*), together with the short-faced hyaena (*Pachycrocuta brevirostris)* present in the Cradle of Humankind caves (Brain, 1981; Keyser, 1991; Keyser and Martini, 1991; Watson, 1993; Turner, 1997; Pickering, 1999; Mutter *et al*., 2001; de Ruiter, 2003; Kibii, 2004; Pickering *et al*., 2004a; Gommery *et al*., 2008, 2012; Reynolds, 2010) (Table 2.3) were also occupying caves and collecting bones.

Hyaenas use caves as resting places, retreats, breeding dens and lairs. They also occasionally hide their food in water, and since the dolomitic caves of the Cradle

sometimes have small water pools, those might be used by the spotted hyaena as a cache. In the lairs, the adult hyaenas will bring carcasses or parts of carcasses to feed the cubs. The uneaten parts and the leftover bony parts of the prey will therefore accumulate in caves, together with regurgitated bone fragments and their faeces, which can fossilize (Backwell *et al*., 2009; Berger *et al*., 2009). Hyaenas have jaws powerful enough to carry heavy carcasses or skeletal parts inside caves. As scavengers (and effective hunters in the case of *C. crocuta)* their prey spectrum is very diverse, from small antelopes with a live weight of 0-23 kg, where the upper limit is represented by a large female duiker (*Silvicapra* sp.), to Class III antelopes in the range 84-296 kg, where the upper limit is represented by a blue wildebeest (*Connochaetes gnou*), and even Class IV, reflecting animals weighing more than 296 kg, including eland (*Taurotragus oryx*) or buffalo (*Syncerus caffer*) (following Brain, 1974). They are also able to carry parts of very large animals, such as elephants (Kuhn, 2006). Therefore, the range of their diet is broad and results in abundant bone remains in the lair (Brain, 1981; Skinner and van Aarde, 1981, 1991; Lacruz and Maude, 2005; Skinner and Chimimba, 2005; Kuhn, 2006).

For hyaenids, Pickering (2002) maintains that the following criteria, when found together, are indisputable evidence of a hyaena-generated assemblage in a cave: bone modification (tooth pits and punctures), occurrence of cylindrical shafts (either whole cylinders or splintered shaft fragments) and high carnivore/ungulate ratio. Kuhn *et al*. (2010) argue that none of these criteria, when taken alone, can constitute direct evidence of a hyaena-generated assemblage; it is rather the combination of several lines of evidence, which can prove that hyaenids have accumulated the bones. The presence of juvenile hyaenids (Cruz-Uribe, 1991; Klein *et al*., 1991; Brugal *et al*., 1997; Pickering, 1999; Kuhn *et al*., 2010), coprolites and digested remains (Pickering, 2002) constitute direct evidence of cave occupation by hyaenas.

**Table 2.3**. Extinct species of large carnivores present in Plio-Pleistocene sites from the Cradle of Humankind.

| Family | Species | Sites | References |
|---|---|---|---|
| **HYAENIDAE** | *Chasmaporthetes silberbergi* | Minnaar's; Sterkfontein Silberberg Grotto and Member 4 | Turner, 1997; Pickering *et al*., 2004a; Gommery *et al*. 2012 |
| | *Chasmaporthetes nitidula* | Swartkrans Members 1-3; Sterkfontein Member 2, Member 4, Member 5 and Jacovec Cave; Haasgat; Drimolen | Keyser, 1991; Keyser and Martini, 1991; Watson, 1993; Turner, 1997; Pickering, 1999; de Ruiter, 2003; Kibii, 2004; Pickering *et al*., 2004a; O'Regan and Menter, 2009 |
| | *Pachycrocuta brevirostris* | Kromdraai A, Bolt's Farm Femur Dump, Sterkfontein Member 4 and Member 5, Gladysvale | Turner, 1997; Mutter *et al*., 2001; Gommery *et al*., 2008; Reynolds, 2010 |
| **FELIDAE** | *Dinofelis barlowi* | Sterkfontein Member 4, Member 5 and Silberberg Grotto; Minnaar's, Malapa, Bolt's Farm | Brain, 1981; Cooke, 1991; Turner, 1997; Pickering *et al*., 2004a; Lacruz *et al*., 2006; Gommery *et al*., 2008, 2012; Kuhn *et al*., 2011 |
| | *Dinofelis piveteaui* | Gladysvale, Motsetse, Kromdraai A, Drimolen | Berger and Lacruz, 2003; Lacruz *et al*., 2006; O'Regan and Menter, 2009 |
| | *Megantereon whitei* | Sterkfontein (Silberberg Grotto, Member 4), Swartkrans (Member 1 Hanging Remnant and Member 3), Kromdraai A | Turner, 1987, 2004; de Ruiter *et al*., 2009 |
| | *Megantereon cultridens* | Swartkrans Member 1 Hanging Remnant and Member 3; Sterkfontein Silberberg Grotto, Members 4 and 5 | Watson, 1993; Turner, 1997; de Ruiter, 2003; Pickering *et al.*, 2004a |
| | *Homotherium latidens* | Sterkfontein (Jacovec Cavern, Members 4 and 5), Swartkrans Member 2 | Kibii, 2004; Turner, 1997; Reynolds, 2010 |

Avian biotic agents: birds of prey

Owls accumulate bones in caves and cave entrances but do not prey upon large animals. Hominins and other large-bodied primates fall outside of their diet range. On the other hand, eagles are known to prey upon animals much larger than themselves, up to the size of a bushbuck (Maclean, 1985; Sanders *et al*., 2003).

Eagles do not occupy caves, but they may select trees or rocky outcrops above cave openings to build their nest. They bring back animal carcasses to their nest where they consume them. Hence, the uneaten and the regurgitated remains can accumulate in the cave located below the nest and contribute to the bone accumulation process within the cave system (Brain, 1981; Andrews, 1990). Various species of eagle are well-known predators of monkeys, such as red-tailed monkeys (*Cercopithecus ascanius*), L'hoest monkeys (*Cercopithecus lhoesti*), red colobus (*Piliocolobus badius*), black and white colobus (*Colobus guereza*), grey-cheeked mangabeys (*Lophocebus albigena*) and olive baboons (*Papio anubis*) (Maclean, 1985; Sanders *et al*., 2003; McGraw *et al*., 2006; Trapani *et al*., 2006). The contribution of large-bodied eagles to the accumulation of primate remains in fossil assemblages has been proposed by Berger and colleagues (Berger and Clarke, 1995; Berger, 2006; Berger and McGraw, 2007) who interpret modifications on the Taung child skull as evidence of predation by a large bird of prey, possibly an African crowned hawk eagle (*Stephanoaetus coronatus*).

Other biotic agents

*Porcupines*

Porcupines collect bones and occupy caves. They have contributed to some extent to the accumulation of some faunal remains in most Plio-Pleistocene fossil assemblages, but they are not regarded as a major taphonomic agent (Maguire *et al*., 1980; Brain, 1981, 1993).

*Small carnivores*

A large variety of small carnivores including canids, small felids, mustelids, viverrids and herpestids can occupy or occasionally frequent caves and cave entrances (Skinner and Chimimba, 2005; Bountalis, 2011; C. Steininger, pers. comm.). Their remains are found in the southern African Plio-Pleistocene assemblages (Brain, 1981; Watson, 1993; Pickering, 1999; de Ruiter, 2003; de Ruiter *et al*., 2009; Kuhn *et al*., 2011; Hartstone-Rose *et al*.,

2013; see Table 2.4), but whether they have contributed to the bone accumulation process is difficult to establish. They can definitely not hunt hominins nor carry large skeletal elements inside caves (Pickering, 1999), but can probably scavenge on animal carcasses and therefore theoretically leave some chewing and breakage marks on bones. Nevertheless, the bone collecting behaviour and the taphonomic signature of small carnivores is very poorly documented (Andrews, 1990). Their contribution is never mentioned in the literature as an important cause of primate bone accumulation in a fossil deposit. The only case published where a small-size carnivore has been identified as a possible taphonomic agent in cave deposits, is at Cooper's D where tooth marks observed on a fragmentary mandible of *Paranthropus robustus* have been attributed to a small canid such as a jackal (de Ruiter *et al*., 2009).

**Table 2.4**. Small carnivore species whose remains have been recovered in the Plio-Pleistocene cave deposits of the Cradle of Humankind.

| Family | Species | Common name |
|---|---|---|
| **CANIDAE** | *Canis mesomelas* | Black-backed jackal |
| | *Vulpes chacma* | Cape fox |
| | *Vulpes skinneri* | extinct fox |
| **FELIDAE** | *Felis serval* | Serval |
| | *Felis caracal* | Caracal |
| | *Felis lybica* | African wild cat |
| | *Felis nigripes* | Black-footed cat |
| **HERPESTIDAE** | *Atilax paludinosus* | Marsh mongoose |
| | *Suricata suricatta* | Suricate/Meerkat |
| | *Cynictis penicillata* | Yellow mongoose |
| | *Paracynictis selousi* | Selous' mongoose |
| | *Herpestes ichneumon* | Large grey mongoose |
| | *Herpestes sanguineus* | Slender mongoose/Black-tipped mongoose |
| | *Ichneumia albicauda* | White-tailed mongoose |
| | *Galerella sanguinea* | Slender mongoose |
| | *Mungos mungo* | Banded mongoose |
| **VIVERRIDAE** | *Genetta tigrina* | South African large-spotted genet |
| | *Civettictis sp.* | African civet |
| **MUSTELIDAE** | *Aonyx capensis* | African clawless otter |
| | *Mellivora sivalensis* | Extinct badger |
| | *Mellivora capensis* | Honey badger |
| | *Poecilogale sp.* | Weasel |

*Suids*

Bushpigs (*Potamochoerus larvatus*) and warthogs (*Phacochoerus africanus*) are omnivorous, scavenge meat and can even in some cases hunt small prey such as chicken (Skinner and Chimimba, 2005). The reasons why African suids occupy caves are not well understood, but cases have been reported of warthogs going inside caves (Brain, 1981; Bountalis, 2011), most likely for protection and thermoregulation. There are even some cases of cohabitation in the same cave between warthogs and spotted hyaenas (Brain, 1981). Even though there is no published data concerning the taphonomic impact of suids in South African cave deposits, their role as potential bone accumulating and modifying agents should be taken into account, and warrants further investigation.

Occupation of caves by hominin and non-hominin primates

Brain has proposed the idea of a "sleeping-site scenario" for primates, including early hominins, which could contribute to explaining the abundance of their remains in some of the Plio-Pleistocene sites of the Cradle of Humankind, especially Sterkfontein and Swartkrans (Brain, 1975, 1981, 1993). If primates occupy caves, natural death occurring inside could lead to the presence of their bones within fossil assemblages. Studies on modern baboons (Altmann and Altmann, 1970; Gow, 1973; Busse, 1980; Brain, 1981; Hamilton, 1982; Mc Grew *et al*., 2003) document the selection by these animals of specific sleeping sites such as tall trees, cliff edges or narrow cave entrances, inaccessible to predators. A recent study (Barrett *et al*., 2004) on modern chacma baboons (*Papio hamadryas ursinus*) reveals that this species commonly occupies caves because it provides access to a source of water. They also use caves to regulate their body temperature as well as to obtain some nutrients from the soil of the cave (geophagy) (Barrett *et al*., 2004). Chimpanzees (*Pan troglodytes verus*) are also known to occasionally frequent caves for the same reasons (Pruetz, 2007). It is therefore conceivable that Plio-Pleistocene primates were using the cave openings for the same purposes. This has been suggested by Brain (1981, 1993) and others (Pickering *et al*., 2004b; Reynolds *et al*., 2011; Val *et al*.,

submitted) as a possible explanation for the presence of hominins and other primates within the South African cave deposits, in particular to explain the high number of non-hominin primates at Swartkrans Member 1 (Hanging Remnant and Lower Bank; Brain, 1981, 1993) and to some extant at Cooper's D (Val *et al*., submitted). Like hominins, they would occupy the entrance of the cave to sleep. The less agile individuals might venture inside the cave and fall in a vertical shaft or not find their way out. This would lead to an attritional mortality profile. In the case that the cave was already occupied by a carnivore, it is also possible that the primates were preyed upon inside the cave.

The earliest direct evidence of cave occupation by hominins dates back to about 1.0 to 1.5 Ma. It consists of evidence of butchery practices conducted inside the cave, associated with defleshing, cooking or consumption. At Wonderwerk Cave, indications of cave use by hominins take the form of burnt bones and ashed plant remains found *in situ* in the deposit, constituting the earliest evidence of the controlled use of fire (Berna *et al*., 2012). At Swartkrans, cut marks on bone fragments (Members 2 and 3; Brain, 1981; Pickering *et al*., 2004d), as well as burnt bones (Member 3; Brain and Sillen, 1988) and the distribution of Early Stone Age tools (Clark, 1993; Backwell and d'Errico, 2003) have been identified and interpreted as indications of hominin presence in the cave. All three deposits are contemporaneous and have been dated at about 1.0 Ma. The Wonderwerk Cave evidence of fire control is found in the Acheulean deposit, associated with Early Stone Age lithic tools (Berna *et al*., 2012). At Swartkrans Member 2, the cut-marked bones are associated with early *Homo* (possibly *H. erectus*) and *Paranthropus* (Brain, 1981; Grine, 1989, 1993) while at Swartkrans Member 3, cut marks and burnt bones are associated with *P. robustus* remains (Brain, 1981; Grine, 1989, 1993). The occurrence of bone tools inside cave deposits (Sterkfontein, Swartkrans Member 1 Lower Bank, Members 2 and 3 and Drimolen), is always associated with *P. robustus* remains (Brain and Shipman, 1993; Backwell and d'Errico, 2001, 2003, 2008; d'Errico *et al*., 2001). Backwell and d'Errico (2003) concluded that hominins introduced bone tools inside the cave when Swartkrans Member 3 was deposited, where a consistent amount of burnt bones, a number of faunal

remains with clear cut marks, and evidence suggesting the presence of a flattened area were found (Brain, 1993; Brain and Sillen, 1988).

When these forms of evidence are absent, the occurrence of hominin remains in cave deposits is interpreted as the result of carnivore predation, accidental falling inside a shaft, or washing in from the surface. The "shift in the balance of power hypothesis" first proposed by Brain (1981, 1993) suggests a long evolutionary pattern explaining the presence of hominin remains in cave deposits, from prey whose bones were accumulated in caves by carnivores to active hunters occupying the caves and conducting inside different social and technological activities, including butchery.

## 2. HOMININ TAPHONOMY IN PALAEOLAKE AND FLUVIAL CONTEXTS

### 2.1. Actualistic data on bone transport in water

#### *2.1.1. Introduction*

Many studies have approached the question of bone transport in a fluvial context (Voorhies, 1966, 1969; Dodson, 1973; Hanson, 1980; Behrensmeyer, 1975, 1982, 1988; Boaz and Behrensmeyer, 1976; Smith, 1980, 1993; Boaz, 1994; Coard and Dennell, 1995; Coard, 1999), but a review of the literature reveals that no experimental study has been conducted on bones in a stagnant pool of water or in a closed space imitating a cave environment. However, the available studies offer elements for discussion, such as transport potential, and orientation of the bones in water that can be useful to understand the behaviour of skeletal remains within a liquid environment. As such, a literature review on the transport potential of bones in fluvial contexts is presented.

#### *2.1.2. The experiments*

Experimental studies conducted on bone transport in water (Voorhies, 1966; Boaz and Behrensmeyer, 1976; Hanson, 1980; Coard and Dennell, 1995; Coard, 1999) have used both modern human (Boaz and Behrensemeyer, 1976) and other mammal bones: sheep (*Ovis aries*) and coyote (*Canis latrans*) (Voorhies, 1966), dog (*Canis familiaris*), mouflon

sheep (*Ovis musimon*) and pig-tailed macaque (*Macaca nemestrina)* (Coard and Dennell, 1995; Coard, 1999). All these studies were conducted using modern bones in a recirculating flume positioned horizontally, with different dimensions and flow velocity (Table 2.5).

**Table 2.5**. Dimensions and flow velocity of the recirculating flumes used in the experimental bone transport in water studies.

| Experiment | Width (m) | Length (m) | Depth (m) | Flow velocity |
|---|---|---|---|---|
| **Voorhies, 1969** | 1.21 | 13.72 | ND | 1.52 m/s |
| **Boaz and Behrensmeyer, 1976** | 0.31 | 12.2 | 0.152 | 0.31 cm/s |
| **Coard and Dennell, 1995** | 0.31 | 7.5 | 0.26 | 0.30 m/s |
| **Coard, 1999** | 0.31 | 7.5 | ND | ND |

*ND: not documented.*

Factors influencing bone transport potential

The results of these studies show that different types of bones have different transport potential. The factors that seem to influence the transportability of bones are described below.

*Shape*

The shape of the skeletal elements was proposed *theoretically* as an important factor conditioning bone transport potential in water by Hill and Walker (1972), and has been *experimentally* proved to influence the transport potential of bones in water (Boaz and Behrensmeyer, 1976; Hanson, 1980; Shipman, 1981). Bones presenting a rounded shape and/or some cavities (i.e. cranium, sacrum, vertebrae) have a better transport potential than elongated and/or solid bones (i.e. long bones, clavicles, tarsals, patellae, teeth). The human crania have the highest transport potential in Boaz and Behrensmeyer's experiment. This is mostly due to the shape of this element, which does not offer any resistance to the current and is transported in a rolling motion, as fast as the current moves. The variations in shape between the different crania tested in the various studies could explain the different results obtained; from the coyote and sheep crania remaining

in the lag group in Voorhies's experiment to the human crania being the fastest element in Boaz and Behrensmeyer's experiment.

*Density*

Density has also been shown to have an impact on the transport potential of bones (Voorhies, 1969; Behrensmeyer, 1975; Boaz and Behrensmeyer, 1976; Coard and Dennell, 1995; Coard, 1999). Elements with a low density (i.e. with spongy bone more volumetrically abundant than compact bone, such as the sacrum and vertebrae) present a better transport potential (Group I of Voorhies and the cranium) than the more compact and dense bones (i.e. long bones, mandibles, tarsals and teeth) (Groups II and III of Voorhies minus the cranium). Coard and Dennell (1995) and Coard (1999) show that density is an important factor that influences the transport potential (supported by statistical analysis of the results), especially of articulated elements.

*Disarticulated versus partially or fully articulated skeletal elements*

The experiments conducted by Coard and Dennell (1995) show that for the three species tested (dog, mouflon sheep and pig-tailed macaque), the articulated parts are easily transported and even present a higher transport potential than the disarticulated skeletal elements. For instance, in the case of the dog, when disarticulated, neither the cranium nor the mandible is transported, whereas the articulated cranium-mandible is. The same is observed for the scapula. While the scapula alone remains in the lag group, the combined scapula-forelimb presents a good transport potential. In Coard's (1999) experiment, the same is observed, with disarticulated bones showing a lesser transport potential than the articulated parts.

*Surface area*

The surface area (linked to the higher transport potential of articulated parts) also influences the transport potential of bones (Coard and Dennell, 1995; Coard, 1999). The

larger the surface, the higher the transport potential; a large surface means more area on which the water can exert pressure and therefore move the bones.

*Nature of the substrate*

The different substrates used by Voorhies (fine-grained sand) and Boaz and Behrensmeyer (coarse-grained sand) influenced the transport potential of the bones. The crania used by Voorhies filled with fine sand and therefore became immobile. Hanson (1980) argues that if the cohesion between the substrate and the bone is strong, then the bone is less likely to move and vice-and-versa. In other words bones tend to get easily embedded in silt and mud, and be more mobile on sand or rock.

*Dry versus wet bones*

Dry bones have a better transport potential than wet ones (Coard, 1999), partly because they can be transported by floating and therefore travel as fast as the water current, whereas wet bones tend to sink more easily and remain on the bed of the flow. Boaz and Behrensmeyer (1976) note that statistically speaking the weight in water and the volume of the considered skeletal parts is not significantly linked to the velocity. However, Coard (1999) demonstrates that both wet and dry volume have a positive coefficient with velocity.

Review of transport potential per anatomical element

Tables 2.6, 2.7 and 2.8 summarise literature about the transport potential for each disarticulated body part.

**Table 2.6**. Transport potential of skeletal elements considered in the literature.

| Skeletal part | | *Voorhies 1969* | *Boaz & Behrensmeyer 1976* | *Coard & Dennell 1995 (dog)* | *Coard & Dennell 1995 (sheep)* | *Coard & Dennell 1995 (macaque)* | *Coard 1999* |
|---|---|---|---|---|---|---|---|
| **Cranium (complete)** | | 0 | + | 0 | + | + | + |
| **Skull fragments** | | ND | 0 | ND | ND | ND | ND |
| **Mandibles** | | 0 | 0 | 0 | 0 | 0 | 0 |
| **Isolated teeth** | | ND | 0 | ND | ND | ND | ND |
| **Vertebrae** | *Atlas* | + | 0 | + | + | + | 0 |
| | *Axis* | + | ND | 0 | + | + | 0 |
| | *Cervical* | + | ND | + | + | + | + |
| | *Thoracic* | + | + | + | + | + | + |
| | *Lumbar* | + | ND | 0 | + | + | + |
| **Ribs** | | + | 0 | 0 | 0 | + | + or 0 |
| **Sacrum** | | + | + | + | + | + | + |
| **Clavicles** | | ND | 0 | ND | ND | ND | ND |
| **Sternum** | | + | + | ND | ND | ND | ND |
| **Scapulae** | *Complete* | + or 0/+ | ND | 0 | 0 | 0 | + or 0 |
| | *Acromion* | ND | 0 | ND | ND | ND | ND |
| **Humeri** | *Complete* | 0/+ | ND | 0 | + | 0 | + or 0 |
| | *Proximal* | ND | + | ND | ND | ND | ND |
| | *Distal* | ND | 0 | ND | ND | ND | ND |
| **Ulnae** | *Complete* | + or 0/+ | ND | 0 | 0 | 0 | + or 0 |
| | *Proximal* | ND | + | ND | ND | ND | ND |
| **Radii** | *Complete* | 0/+ | ND | 0 | ND | 0 | ND |
| | *Proximal* | ND | + or 0 | ND | ND | ND | ND |
| **Pelvises** | *Complete* | 0/+ | ND | 0 | + | 0 | + or 0 |
| | *Acetabulum* | ND | + | ND | ND | ND | ND |
| **Patellae** | | ND | 0 | ND | ND | ND | ND |
| **Femurs** | *Complete* | 0/+ | ND | 0 | + | 0 | 0 |
| | *Head* | ND | 0 | ND | ND | ND | ND |
| **Tibiae** | *Complete* | 0/+ | ND | 0 | 0 | 0 | 0 |
| | *Proximal* | ND | + | ND | ND | ND | ND |
| **Fibulae** | | ND | ND | 0 | ND | 0 | ND |
| **Calcanei** | | ND | + | 0 | + | 0 | 0 |
| **Astragali** | | ND | + | 0 | + | 0 | 0 |
| **Naviculars** | | ND | ND | 0 | 0 | + | 0 |
| **Cuboids** | | ND | + | ND | ND | ND | ND |
| **Metapodials** | | 0/+ | + | + | + | + | 0 |
| **Phalanges** | *1st* | + or 0/+ | ND | 0 | + | 0 | 0 |
| | *2nd* | + or 0/+ | ND | 0 | + | 0 | 0 |
| | *3rd* | + or 0/+ | ND | + | + | 0 | 0 |

*0: no transport potential; 0/+: low transport potential; +: good transport potential; ND: not documented.*

**Table 2.7**. Velocity (cm/s) recorded in the literature for each skeletal element.

| Skeletal part | | *Boaz & Behrensmeyer 1976* | *Coard & Dennell 1995 (dog)* | *Coard & Dennell 1995 (sheep)* | *Coard & Dennell 1995 (macaque)* |
|---|---|---|---|---|---|
| **Cranium complete** | | 19.61 | 0 | 15.79 | 15.41 |
| **Skull fragments** | | 0 | ND | ND | ND |
| **Mandibles** | | 0 | 0 | 0 | 0 |
| **Isolated teeth** | | 0 | ND | ND | ND |
| **Vertebrae** | *Atlas* | 0 | 11.28 | 17.51 | 8.77 |
| | *Axis* | ND | 0 | 16.73 | 15.68 |
| | *Cervical* | ND | 8.59 | 15.57 | 13.20 |
| | *Thoracic* | 9.14 | 10.54 | 14.80 | 13.51 |
| | *Lumbar* | ND | 0 | 20.83 | 12.82 |
| **Ribs** | | 0 | 0 | 0 | 15.15 |
| **Sacrum** | | 14.33 | 9.89 | 17.24 | 14.56 |
| **Clavicles** | | 0 | ND | ND | ND |
| **Scapulae** | *Complete* | ND | 0 | 0 | 0 |
| | *Acromion* | 0 | ND | ND | ND |
| **Humeri** | *Complete* | ND | 0 | 7.28 | 0 |
| | *Proximal* | 8.84 | ND | ND | ND |
| | *Distal* | 0 | ND | ND | ND |
| **Ulnae** | *Complete* | ND | 0 | 0 | 0 |
| | *Proximal* | 5.18 | ND | ND | ND |
| **Radii** | *Complete* | ND | 0 | ND | 0 |
| | *Proximal* | 1.68 | ND | ND | ND |
| **Pelvises** | *Complete* | ND | 0 | 16.98 | 0 |
| | *Acetabulum* | 9.15 | ND | ND | ND |
| **Patellae** | | 0 | ND | ND | ND |
| **Femurs** | *Complete* | ND | 0 | 5.64 | 0 |
| | *Head* | 0 | ND | ND | ND |
| **Tibiae** | *Complete* | ND | 0 | 0 | 0 |
| | *Proximal* | 2.44 | ND | ND | ND |
| **Fibulae** | | ND | 0 | ND | 0 |
| **Calcanei** | | 11.59 | 0 | 9.87 | 0 |
| **Astragali** | | 7.32 | 0 | 7.41 | 0 |
| **Naviculars** | | ND | 0 | 0 | 16.85 |
| **Cuboids** | | 12.50 | ND | ND | ND |
| **Metapodials** | | 7.01 | 12.00 | 6.07 | 13.98 |
| **Phalanges** | *1st* | ND | 0 | 11.98 | 0 |
| | *2nd* | ND | 0 | 19.32 | 0 |
| | *3rd* | ND | 11.90 | 11.16 | 0 |

*ND: not documented.*

**Table 2.8.** Transport potential and mean velocity (cm/s) for each complete, disarticulated skeletal element (after Voorhies, 1969; Boaz and Behrensmeyer, 1976; Coard and Dennell, 1995).

| Skeletal element | Transport potential | Mean velocity |
|---|---|---|
| **Sacrum** | ++ | 14.00 |
| **Cervical** | ++ | 12.45 |
| **Thoracic** | ++ | 12.00 |
| **Sternum** | ++ | ND |
| **Cranium** | + | 16.94 |
| **Lumbar** | + | 16.82 |
| **Atlas** | + | 12.52 |
| **Metapodials** | + | 9.76 |
| **Pelvis** | 0/+ | 16.98 |
| **Axis** | 0/+ | 16.20 |
| **Third phalanges** | 0/+ | 11.53 |
| **Calcaneum** | 0/+ | 10.73 |
| **Astragalus** | 0/+ | 7.36 |
| **Humerus** | 0/+ | 7.28 |
| **Second phalanges** | 0+ | 19.32 |
| **Ribs** | 0+ | 15.15 |
| **First phalanges** | 0+ | 11.98 |
| **Radius** | 0+ | ND |
| **Ulna** | 0+ | ND |
| **Femur** | 0+ | 5.64 |
| **Tibia** | 0+ | ND |
| **Navicular** | 0+ | 0 |
| **Fibula** | 0 | 0 |
| **Patella** | 0 | 0 |
| **Scapula** | 0 | 0 |
| **Clavicle** | 0 | 0 |
| **Isolated tooth** | 0 | 0 |
| **Mandible** | 0 | 0 |

*++: transportable in all the cases considered; +: transportable in the majority of the cases (one or two exceptions); 0/+: low transport potential (half +, half 0); 0+: in the lag group in the majority of the cases (one exception); 0: always in the lag group.*

These theoretical results do not explain everything. For instance, metapodials present the same characteristics (in terms of density and shape) as long bones and yet they belong to the transportable group. Some differences between the same type of experiments (same protocol, same fluid used) are difficult to explain based only on the criteria of shape and density. For instance, the mouflon sheep, macaque and human crania are in the transportable group, whereas the dog cranium is in the lag one (Coard and Dennell, 1995). However, as already mentioned by Coard and Dennell (1995), the shape of a dog skull, as well as the density, present the same general characteristics as any

of the other skulls, especially the sheep. In the experiment conducted by Voorhies (1969), the cranium of the sheep is in the lag group, but not in the experiment conducted by Coard and Dennell (1995).

Transport in water and orientation of the bones

Within flowing water all bones and bone fragments become aligned and come to rest in a horizontal plane, even at high current velocities (maximum of 1.52 m/s; Voorhies, 1966). Only in cases of torrential turbulent currents, the long bones might come to rest in a subhorizontal or vertical orientation (Voorhies, 1966), but this has never been tested experimentally. The orientation of the elongated bone fragments and long bones parallel to the direction of the current is often cited as evidence of a fluvial channel setting for fossil assemblages (Behrensmeyer, 1975; Shipman, 1981a). This is also demonstrated by experimental studies (Voorhies, 1966, 1969; Boaz and Behrensmeyer, 1976; Coard and Dennell, 1995). Regardless of the initial orientation of the bones when arriving in the fluid, the elongated bones (complete or partial long bones and ribs) tend to orientate parallel to the current (Voorhies, 1969; Boaz and Behrensmeyer, 1976; Coard and Dennell, 1995; Coard, 1999), with the largest end pointing downstream (Voorhies, 1966; Boaz and Behrensmeyer, 1976). This is especially true when the water is deep enough to completely cover the bones. Voorhies (1966) has registered cases when long bones orientate perpendicular to the current when the water flow is shallow and the bones are consequently partly emerged. The innominate bone is a good indicator of water direction, since it invariably orientates parallel to the current with the ilium pointing downstream (Voorhies, 1966; Coard and Dennell, 1995). According to Voorhies (1966) this bone tends to rest upside down, but this was not noted by Coard and Dennell (1995). The scapula is also a good indicator of flow direction and orientates parallel to it (Coard, 1999). Both the pelvis and the scapula loose their preferred orientation when still articulated (Coard, 1999). However articulated vertebrae tend to align with the current. The lower jaw, when rotated by the current, can also orientate according to the flow direction (Voorhies, 1966),

although with a lesser degree of regularity than long bones, due to the less regular shape of mandibles. In deep water, mandibles tend to orientate parallel to the current, whereas in shallow water, they orientate transverse to the current. The attitude of the jaw bone is influenced by the strength of the current; in medium to fast velocities, jaws become stable in a convex-up position (Voorhies, 1966). The crania do not show any downstream alignement since they are either in the lag group (Voorhies, 1966) or rolling (Boaz and Behrensmeyer, 1976). The small and flat bones remain stable and do not show any preferential orientation according to the water flow (Voorhies, 1966; Boaz and Behrensmeyer, 1976).

## 2.2. Hominin taphonomy in lacustrine and fluvial context

### *2.2.1. Introduction*

The majority of the hominins and associated fauna from Central and East Africa were preserved in fluvial and lacustrine environments (Behrensmeyer, 1975, 2008; Johanson *et al*., 1982; Walker, 1993; White *et al*., 1995; Pickford and Senut, 2001; Vignaud *et al*., 2002; Egeland *et al*., 2007). A brief literature review of early hominin taphonomy in different fossil localities from Central and East Africa is provided below.

### *2.2.2. Case studies*

#### *Sahelanthropus tchadensis* (Toumaï) and associated fauna

The remains of the earliest known representative of the hominin lineage, *S. tchadensis* (Brunet *et al*., 2002), were recovered together with abundant fauna (constituting the TM266 assemblage) in the Djurab Desert, northern Chad (Figure 2.2). The hominin remains include six specimens (one complete cranium, a fragmentary right mandible, a symphyseal fragment and three isolated teeth), representing a minimum number of one individual (Brunet *et al*., 2002). The assemblage is dated between 6 and 7 Ma, and is composed of numerous aquatic taxa, such as fish, crocodiles, amphibians and

hippopotamids (Vignaud *et al*., 2002), all indicative of the proximity of a lake. On the other hand, the occurrence of primates, rodents, elephants, equids and bovids also show the existence of gallery forests and savannah in the vicinity (Vignaud *et al*., 2002). The assemblage formed over a short period of time and has an autochthonous origin. There is no evidence of water polishing and no sorting, which shows limited (Le Fur *et al*., 2009) or no fluvial transport (Vignaud *et al*., 2002). The accumulation of the assemblage could either be the result of a catastrophic event, as indicated by the presence of some specimens still in articulation and the variety in the bone and tooth wear, or an attritional process, or a combination of both (Le Fur *et al*., 2009). The state of preservation of the hominin specimens is variable. The skull is near complete but very crushed, while the other remains are undistorted and the bone surfaces generally well preserved (Brunet *et al*., 2002). There is no mention of carnivore or other biotic damage on the hominin remains.

*Orrorin tugenensis* and associated fauna

The fragmentary remains of *O. tugenensis* and associated animals were found in 2001 in the Miocene Lukeino Formation, Tugen Hills, Kenya (Senut *et al*., 2001) (Figure 2.2) and have been dated around 6 Ma (Sawada *et al*., 2002). They were recovered in fluvial and shallow lake deposits (Pickford and Senut, 2001). The hominins are represented by 13 fossils, belonging to a minimum of five individuals (Senut *et al*., 2001). The palaeoenvironmental reconstructions indicate a landscape composed of open woodland, with denser strands of trees in the vicinity, possibly fringing the lake margin and streams that drained into the lake (Pickford and Senut, 2001). Concerning the taphonomy of the assemblage, it seems that different events led to the preservation of the bones. Some fossils show evidence of carnivore damage, including the hominin femurs. Numerous fossils are covered with a thin pellicle of bacterial or algal origin, indicating that they fell into the water and were covered with algae before being buried in the sediment. On the

other hand, some fossils, including some hominin specimens, are highly weathered, indicating a long time of exposure before burial (Pickford and Senut, 2001).

*Ardipithecus ramidus* and associated fauna

*Ar. ramidus*, whose remains were first identified in 1992 in Aramis, Middle Awash, in the Ethiopian Afar rift (White *et al*., 1994) (Figure 2.2), is now represented by 109 specimens, belonging to a minimum of 36 individuals, including a near complete female individual, ARA-VP-6/500 (White *et al*., 2009a). The specimens were dated around 4.4 My (White *et al*., 1994) and were recovered in alluvial silty clay of the Lower Aramis Member. The palaeoenvironmental reconstruction suggests the presence of woodland environment with small patches of forest (Louchart *et al*., 2009; White *et al*., 2009b). Taphonomic analysis shows the absence of any damage associated with transport or sorting by water. The rarity of advanced stages of weathering in the fossil assemblage suggests that the time of exposure before burial was short. It also suggests a rapid deposition of the unit. The faunal assemblage is composed of small to large mammals, with some bones showing evidence of carnivore chewing, rodent gnawing and termite damage, as well as fracture and decalcification resulting from exposure to erosion (Louchart *et al*., 2009; White *et al*., 2009a). Based on the tooth marks and body part representation (an overrepresentation of teeth, jaws and limb bone shafts on one hand, and underrepresentation of skull and limb bone epiphyses on the other), hyaenas and other medium to large size carnivores have been identified as important taphonomic agents in the formation of the faunal assemblage. The abundance of small mammal and small bird remains, as well as the type of damage observed on their bones, is interpreted as the result of owl predation and accumulation of regurgitated pellets. The near complete *Ar. ramidus* female individual ARA-VP-6/500 seems to have a slightly different taphonomic history. The remains (MNE=86) include numerous complete or near complete bones characterised by an absence of carnivore damage and weathering. The degree of preservation of the bone surface is very poor, and while the small bones are undistorted, the long bones are

variably crushed (White *et al*., 2009a). The skull is broken into several pieces that were found relatively dispersed, which indicates that the "bones of the carcass came to rest in a shallow swale on the flood plain" and were trampled, which is also visible in the way some larger bones are fragmented and scattered (White *et al.*, 2009a).

*Kenyanthropus platyops* and associated fauna

The remains of *K. platyops* (a near complete skull and a partial left maxilla) and associated fauna were recovered in a mudstone level deposited along the margin of a shallow lake, West Lake Turkana, Kenya, 3.5 Mya (Leakey *et al*., 2001) (Figure 2.2). The vault has been heavily distorted by compression and the bone surface is poorly preserved.

*Australopithecus afarensis* (Lucy)

The near complete skeleton of Lucy (AL-288-1) was recovered in 1974 in the Hadar Formation, Afar Region, Ethiopia (Figure 2.2), and attributed to what was then a new species, namely *Australopithecus afarensis* (Johanson and Taieb, 1976; Johanson *et al*., 1978; Johanson and White, 1979; Johanson and Edey, 1982). The skeleton preserves broken, but also complete or near complete bones, with all the body parts represented (the minimum number of elements preserved, including the teeth, is 42; Johanson and Taieb, 1976). The bone surface is also well preserved and shows no evidence of pre-fossilisation weathering (Johanson and White, 1979; Johanson *et al.*, 1982). As with the other hominins and associated fauna recovered from the Hadar Formation, the remains of Lucy were recovered in sediments consistent with lacustrine and lake margin deposits (Johanson *et al*., 1982). It has been proposed that Lucy's remains were collected from secondary deposit, after having been eroded out of a palaeochannel sandstone, and transported by a modern stream (Johanson *et al*., 1982; Radosevich *et al*., 1992).

*Australopithecus afarensis* individuals from AL-333 locality

The locality AL-333 in the Hadar Formation, Afar Region, Ethiopia (4 km northwest of the junction of the Kada Hadar and the Awash River; Figure 2.2), is an excavated area of 33 $m^2$, which has yielded more than 200 fossil bones, including 18 recovered *in situ*. These fossils constitute the remains of a minimum of 13 individuals, including two infants, two juveniles, and nine adults (Johanson *et al*., 1982; Radosevich *et al*., 1992). They have all been attributed to *Au. afarensis* and dated to 3.2 My (Brown, 1982; Sarna-Wojcicki *et al.*, 1985). The fossils are preserved in a primary deposit (palaeosols), and do not show any evidence of any fluvial transport. For instance, a partial articulated food and hand have been recovered, and the body part frequencies show the absence of fluvial sorting of the bones. The weathering state of the assemblage is consistent with stage 1 of Behrensmeyer (1978), and there is no indication of scavenging or predation by carnivores (Radosevich *et al*., 1992). Furthermore, the faunal assemblage is exclusively composed of hominin remains, with the exception of a few fish, reptile and rodent bones (Johanson *et al*., 1982). The taphonomic hypothesis proposed to explain the accumulation of the hominins is a catastrophic event, such as a flood, leading to the simultaneous death of a group of australopithecines. The death would have been followed by a short period (a couple of months) of exposure during which decay and disarticulation took place before the final burial of the skeletons occurred (Johanson *et al*., 1982; Radosevich *et al*., 1992).

Selam (DIK 1-1): a juvenile *Au. afarensis* skull and associated skeleton from Dikika, Ethiopia

The skull and associated skeleton of a juvenile *Au. afarensis* (specimen DIK1/1, nick-named “Selam”) were recovered between 2000 and 2003 in the fluvial sediments of the Sidi Hakoma Member of the Hadar Formation, Ethiopia (Figure 2.2) (Alemseged *et al*., 2006), which date to 3.31-3.35 My (Wynn *et al*., 2006). Based mostly on bone and teeth morphology, DIK 1/1 is considered to be a three year old female australopithecine (Alemseged *et al*., 2006). The near complete skull and articulated mandible were recovered in a block of sandstone matrix, in articulation with the right and left scapulae,

clavicles, cervical, thoracic and first two lumbar vertebrae, many ribs and the first known hyoid in early hominin fossil record (Alemseged *et al*., 2006). The hominin assemblage also includes post-cranial material: left scapula fragment and ribs, manual phalanges, left proximal tibia, a left articulated foot, including the distal fibula and tibia, the talus, calcaneum, tarsals and metatarsals, a right distal femur, associated with patella and proximal tibia, a right humerus, a left distal femur and patella, a left tibia fragment, a left femur fragment, and many rib fragments. Most bones are complete or near complete except for the long bones; they are relatively well preserved, even though they have suffered slight distorsion from sediment pressure (Alemseged *et al*., 2006). The associated non-hominin faunal material recovered in sandstone is dominated by ungulates, with a few carnivore and primate remains. The faunal spectrum is consistent with a mosaic of mesic habitats, including a woody component as well as evidence of open grasslands (Wynn *et al*., 2006). Many non-hominin faunal elements were recovered in articulation and show no evidence of pre-burial weathering (Alemseged *et al*., 2006). The proposed taphonomic scenario for the australopithecine is a quick burial shortly after death (i.e. corpse still intact), probably during a major flood event (Alemseged *et al*., 2006).

Other gracile and robust australopithecines and *Homo habilis* specimens from East Africa

Several hundreds of specimens belonging to gracile (*Australopithecus garhi* and *Australopithecus anamensis*) and robust (*Paranthropus boisei* and *Paranthropus aethiopicus*) australopithecines, and *Homo habilis* have been recovered from various localities in the eastern part of the African continent: Hadar Formation, Middle Awash, Omo Valley (Ethiopia), Turkana Basin, Koobi Fora (Kenya), and Olduvai Gorge (Tanzania) (Figure 2.2). These specimens are represented by fragmentary isolated skull and post-cranial elements, very rarely by complete bones and never by complete or near-complete skeletons. There are only a few cases of articulated bones preserved, such as an articulated right hand of a juvenile hominin, namely the holotype of *H. habilis* (specimen OH7; Leakey *et al*., 1964) and an articulated foot, the paratype of *H. Habilis* (specimen

OH8; Leakey *et al*., 1964, Susman and Stern, 1982). The majority of these specimens was recovered in lacustrine, floodplain or old riverbed environments and have undergone different taphonomic destructive processes, such as weathering, trampling, carnivore activity and dispersal by water (Behrensmeyer, 1975, 2008; Johanson *et al*., 1982; Potts, 1988; Egeland *et al*., 2007).

The Nariokotome *H. erectus* skeleton (KNM-WT 15000)

KNM-WT 15000 is a near complete skeleton of *H. erectus*, recovered in the Turkana Basin, near the Nariokotome Sand River, northern Kenya (Figure 2.2). Its remains, found in an ancient floodplain environment within lowland swamp, have been dated to 1.5 Ma (Brown and McDougall, 1993; Fiebel and Brown, 1993). Most of the bones are broken, possibly due to trampling by large mammals. There is no articulation preserved, even though there is some anatomical proximity, such as the left scapula and humerus, and the left ilium and femur. The bones appear to have been dispersed by a gentle current (several metres wide). The presence of a periodontal lesion on the right side of the mandible indicates that the individual could have died because of an infection of the tooth and gum. The absence of carnivore damage as well as weathering argues in favour of burial of the skeleton soon after death, either because it fell into the swamp or because it was washed into it by a minor flood. After disarticulation, trampling by large mammals and dispersal by water, the different bones eventually became embedded in the swamp mud where they fossilised (Walker, 1993).


**Figure 2.2**. Early hominin fossil localities in Central and East Africa (after Egeland *et al*., 2007, modified). The localities mentioned in the text are highlighted in red.

### *2.2.3. Fossil hominins in lacustrine and fluvial contexts: summary*

A certain number of similarities amongst the different examples mentioned above can be highlighted (Table 2.9).

**Table 2.9**. Summary of the preservation of some early hominins recovered in Central and East Africa.

| Species | MNI | Fragmentation | Completeness | Elements in articulation | Taphonomy | References |
|---|---|---|---|---|---|---|
| ***S. tchadensis*** | 1 | fragmentary remains, except the near complete skull | one skull, 12 teeth, a right hemi-mandible = (14/183)*100 = 7.65% | no | no specific agent identified | Brunet *et al*., 2002; Vignaud *et al.*, 2002; Le Fur *et al*., 2009 |
| ***O. tugenensis*** | 5 | no complete bone preserved | [(13*5)/(183*5)]*100 =7.10% | no | carnivores, weathering, | Pickford and Senut, 2001 |
| ***Ar. ramidus*** | 1 | all the bones are complete or near complete for ARA-VP-6/500; fragmentary isolated bone remains for the other individuals | *(ARA-VP-6/500 skeleton):*86 elements<br>%survival: (86/183)*100 = 47%<br>For the whole hominin assemblage:<br>[109/(36*183)]*100= 1.65% | no | trampling | White *et al*., 2009a;<br>Louchart *et al*., 2009 |
| ***K. platyops*** | 2 | skull near complete; left maxilla very fragmentary | 2 remains<br>% survival= (2/183)*100 =1.1% | no | no specific agent identified | Leakey *et al*., 2001 |
| ***Lucy (Au. afarensis)*** | | all bones are broken but the majority are complete or near complete | MNE = 48<br>% survival = (48/183)*100 = 26.2% | no | no weathering, one puncture possibly produced by a carnivore | Johanson and Taieb, 1976; Johanson and Edey, 1982; Johanson *et al*., 1982 |
| ***Au. afarensis*** **individuals from AL-333 locality** | | majority of fragmentary and isolated remains | MNI=13; MNE = 200<br>%survival = [200/(13*183)]*100=8.4% | one partial foot and one partial hand | weathering stage 1, no evidence of carnivore damage | Johanson *et al*., 1982; Radosevich *et al*., 1992 |
| **Selam (DIK-1/1)** ***Au. afarensis*** | | all bones are complete and near complete, except for the long bones | Most elements preserved<br>MNI = 1; MNE = 67<br>%survival<br>[67/(1*171)]*100]=39.2% | one partial foot and skull articulated with mandible and upper body (clavicles, scapulae, vertebrae and ribs) | no weathering, no evidence of carnivore damage | Alemseged *et al*., 2006; Wynn *et al*., 2006 |
| **KNM-WT 15000 (*H. erectus*)** | 1 | most of the bones are broken | - | no | trampling | Walker, 1993 |

The hominin specimens recovered are almost always disarticulated. Complete bones are rare. A common trait is the rapidity of burial, which has protected the hominin specimens from being intensively damaged by taphonomic agents. Hence, carnivore, rodent and weathering damages are rare on these skeletons (Table 2.9). It is noteworthy to remember that the examples mentioned above represent exceptions within the fossil record rather than the rule. Amongst the hundreds of specimens recovered in East Africa, specimens AL-288-1 ("Lucy", *Au. afarensis*), ARA-VP-6/500 (*Ar. ramidus*), DIK-1/1 ("Selam", *Au. afarensis*), and KNM-WT 15000 ("Turkana boy", *H. erectus*) are the *only* individuals represented by near-complete skeletons.

# Chapter 3. Materials

## 1. HOMININ REMAINS

### 1.1. Individuals

The hominin specimens used in this study comprise a collection of 256 fossil bones and teeth (for a complete list of specimens, see Appendix 1). The minimum number of individuals (MNI) is estimated at six. Two individuals (MH1 and MH2) are near complete, whereas the other four individuals are each represented by only a few fragments.

Malapa Hominin 1 (MH1) from Facies E and D was the first individual discovered. It is a juvenile male represented by 101 bones, bone fragments and teeth. The specimens that have been prepared so far include most of the body parts; the skull and the mandible, elements from the upper and the lower limbs, mostly from the right side (scapula and long bone fragments, as well as a few metacarpals, metatarsals, and one phalanx), elements from the axial skeleton (clavicle, vertebrae, ribs, and sacrum) and parts of the pelvis. A block of calcified sediment (UW88-B051) contains hominin bones that are attributed to MH1. This block has not been prepared yet (virtual segmentation in progress) and the bones have so far only been identified using CT scanning images. The quality of the scanning images allows preliminary identification of the bones present inside, which include the left hemi-mandible with the three lower molars (the first two ones erupted and the third one in crypt), the complete left femur, a fibula shaft, the distal part of the right ulna, the left clavicle, at least four complete or near complete ribs, a possible fragment of a radius or rib, the shaft of a long bone (possibly the left humerus), another near complete long bone (a tibia or the distal right femur), a possible distal part of a humerus, and five foot or hand bones.

Malapa Hominin 2 (MH2) is an adult female, represented by 119 bones, bone fragments and teeth. All of the body parts are present, except for the skull. MH2

comprises more articulated specimens than MH1, and a large number of the skeletal elements are complete.

Two remains, namely a distal right humerus (UW88-81) and an associated proximal right ulna (UW88-82) belong to the same individual, possibly an infant. It referred to as MH3. Its remains were recovered from Facies E, just above Facies D, west of it, near to where the *Dinofelis* remains have been recovered.

Malapa Hominin 4 (MH4) is an adult (sex indeterminate) and is composed of a near complete right tibia (UW88-21, the distal tibia fusing with UW88-40, the proximal tibia).

Malapa Hominin 5 (MH5) is a possible other infant (sex indeterminate) and comprises two bones, including a right femur (UW88-175) and an associated unidentifiable bone fragment (UW88-176).

Malapa Hominin 6 (MH6) is an adult represented by a mandible with teeth. These remains are still *in situ* in Pit 2 (Facies F), embedded in the matrix, and have therefore not been issued specimen numbers yet.

Twenty-six other elements do not at present refit with any of the previously mentioned individuals. Two of them were recovered *in situ* in Facies D, while the other 20 are fragmentary bone remains that were recovered during the manual preparation of *ex situ* breccias blocks. They include long bone fragments, elements from the innominate and the mandible, phalanges and metapodials, and rib fragments. For a complete list of the hominin specimens recovered so far, see Appendix 1.

### 1.2. Taxonomic attribution

The remains of the two well-preserved individuals (MH1 and MH2) constitute the Holotype and Paratype of a new hominin species, described by Berger *et al*. (2010). This new species was named *sediba* after the seSotho word for “spring”. It has been placed in the genus *Australopithecus*, but presents a combination of primitive and derived

characters not observed in any of the other australopithecine species (Berger *et al*., 2010; Berger, 2012). The adherence to the genus *Australopithecus* is based on the persistence of primitive characters, such as a small brain-size, long upper arms, gracile morphology of the calcaneum and body dimensions in general (Berger *et al*., 2010; Carlson *et al*., 2011; Kibii *et al*., 2011; Kivell *et al*., 2011; Zipfel *et al*., 2011; Berger, 2012). However, several modern features such as the morphology of the pelvis (Berger *et al*., 2010; Kibii *et al*., 2011), the reduced size of the canines (Berger *et al*., 2010), the development of some human-like parts of the brain (Carlson *et al*., 2011), and the ankle joint (Zipfel *et al*., 2011) show that *Au. sediba* also shares a number of characters with early *Homo*. *Au. sediba* is thus potentially a key-species to understanding the ancestry of the genus *Homo* and the transition from australopithecines to early *Homo*, whether *Homo habilis* or *Homo ergaster* (Berger *et al*., 2010; Berger, 2012).

### 1.3. Stratigraphic provenance of the hominin remains

Subsequent to the discovery of the first hominin remains, fieldwork at the site between 2008 and 2010 focused on collecting all the *ex situ* blocks removed by the miners, which were lying next to the main opening of the site (Figure 3.1). To date, a few *in situ* blocks of calcified sediment have been extracted from the site, and the *in situ* decalcified sediment has undergone excavation and sieving. The majority of the hominin remains (*n.* 205) were found in the *ex situ* blocks (see Appendix 1). However, a significant number of remains (*n.* 51) were still embedded in the matrix within the cave deposit. All of the MH2 *in situ* remains come from Facies D, dated to 1.977 Million years (Figure 3.1.; Dirks *et al*. 2010; Pickering *et al*., 2011), while the *in situ* MH1 remains come from the bottom of Facies E, just above Facies D (P.Dirks, pers. comm.). The MH3 remains were recovered in Facies E, just above Facies D (Figure 3.1). The remains of another individual (MH6, a mandible together with some teeth) are still embedded in Pit 2 in Facies F. The isolated bones of MH4 and MH5 were found in a separate *ex situ* blocks removed by the miners. It is at present difficult to confidently determine their facies of origin.

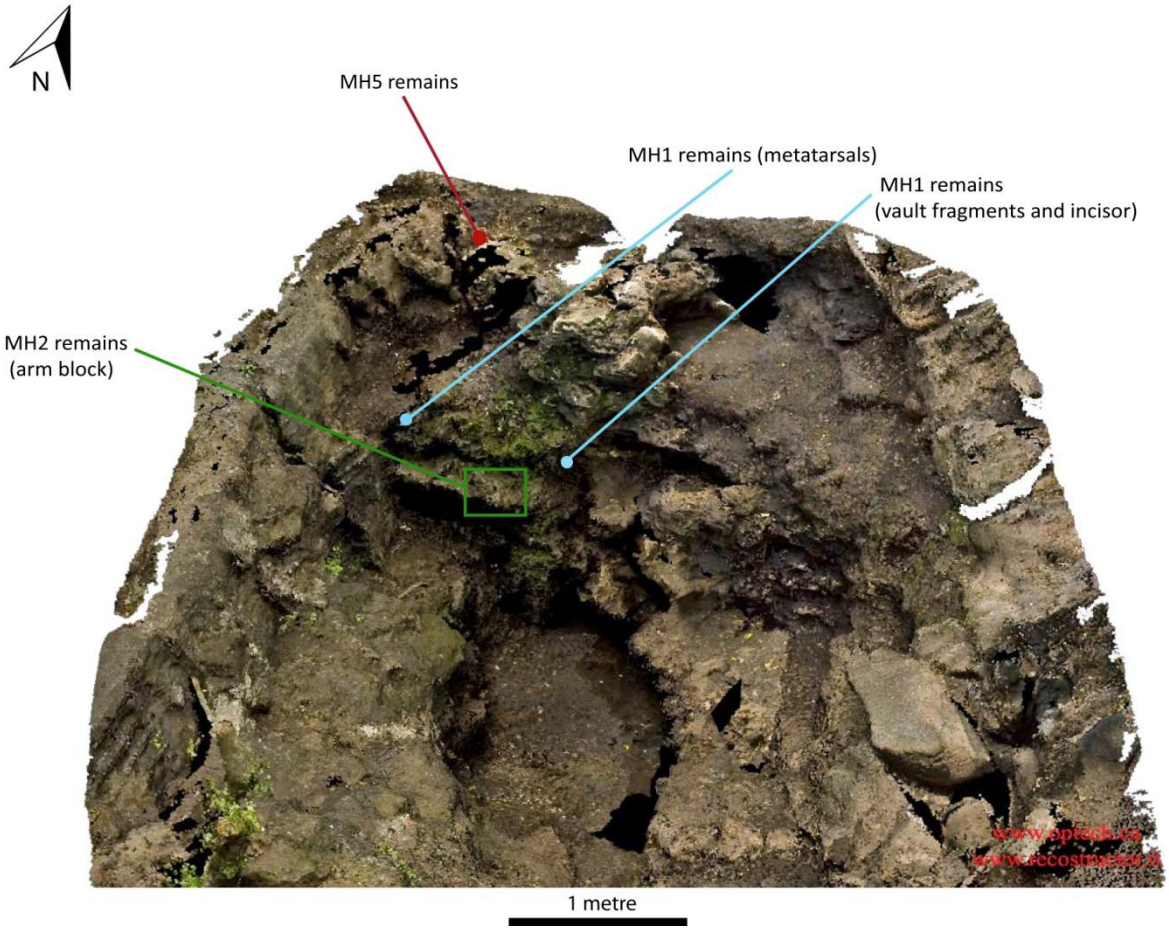



**Figure 3.1.** 3D reconstruction of Pit 1 at the Malapa site showing the mined area and the provenance of the hominin *in situ* remains (image: courtesy of D. Conforti, Optech company, modified).

## 2. NON-HOMININ FAUNAL REMAINS

To date, the total number of identified non-hominin faunal remains is 1061. Preliminary results on the faunal remains have been published (Table 3.1.; Dirks *et al*., 2010; Kuhn *et al*., 2011; Val *et al*., 2011; Hartstone-Rose *et al*., 2013), but the analysis of the whole assemblage is currently in progress. The majority of the remains (*n.* 957) come from *ex situ* blocks of clastic calcified sediments, while 104 remains were recovered *in situ* or during sieving of decalcified sediment.

**Table 3.1**. Identifiable fauna from Malapa (after Dirks *et al.*, 2010 ; Kuhn *et al*., 2011 ; Val *et al*., 2011 ; Hartstone-Rose *et al*., 2013).

| Order | Family | Species | MNI |
|---|---|---|---|
| **CARNIVORA** | Felidae | *Dinofelis* sp. | 1 |
| | | *Dinofelis barlowi* | 1 |
| | | *Panthera pardus* | 1 |
| | | *Panthera* cf. *P. pardus* | 1 |
| | | cf. *Panthera* sp. | 2 |
| | | *Felis nigripes* | 1 |
| | | Felidae indet. | |
| | Hyaenidae | *Parahyaena brunnea* | 2 |
| | | cf. *Parahyaena brunnea* | 1 |
| | | Hyaenidae indet. | |
| | Canidae | Large canidae indet. | 1 |
| | | *Vulpes skinneri* | 1 |
| | Herpestidae | *Atilax* cf. *A. mesotes* | 1 |
| | | cf. Herpestidae | 1 |
| | Viverridae | cf. *Genetta* sp. | |
| **PERISSODACTYLA** | | *Equus* sp. | 1 |
| **ARTIODACTYLA** | | Suidae indet. | 1 |
| | | *Oreotragus* sp. | 1 |
| | | *Megalotragus* sp. | 1 |
| | | *Large-sized alcelaphine* | 1 |
| | | *Tragelaphus* cf. *scriptus* | 1 |
| | | *Tragelaphus* cf. *strepsiceros* | 1 |
| | | *Lepus* sp. | 1 |
| **PRIMATES** | | *Papio* sp. | 1 |
| **TESTUDINES** | | *Chelonia* sp. | 1 |
| **MICROFAUNA** | | *Elephantulus* sp. | 1 |

## 3. OTHER TYPES OF REMAINS

### 3.1. Coprolites

Only one coprolite has been recovered and prepared so far. It was found in an *ex situ* block of calcified sediment (UW88-B020) and tentatively identified as carnivore in origin, and has been used for pollen analysis and palaeoecological assessment (Bamford *et al*., 2010). A few other possible coprolites have been identified in blocks through virtual exploration using Avizo 6.3 software but the preparation of these blocks is still to be done.

### 3.2. Millipedes

One almost complete pill millipede was recovered and given a specimen number (UW88-763).

### 3.3. Insect pupae

Abundant insect pupae were observed outside and inside (i.e. during virtual exploration) blocks of calcified sediment.

### 3.4. Molluscs

One small terrestrial snail is recorded and has been given a specimen number (UW88-1117). It was found in an *ex situ* block (UW88-B999). Two other shells of *Gulella* sp. and one *Achatina* sp. have been identified during the preparation of breccias blocks. They have not been assigned specimen numbers. Numerous other mollusc shells have been observed and await a specimen number.

### 3.5. Seeds

Seeds have been identified in the block that contained the MH2 scapula fragment. They have been virtually extracted using Avizo 6.3 and their identification is currently in progress (Tea Jashashvili, pers.comm.).

### 3.6. Organic residues

Organic material, possibly related to soft tissues, has been identified on some bone remains (Keeling *et al*., in prep.) and is currently under study, to determine its exact origin.

# Chapter 4. Methods

This chapter presents the methods and techniques that were applied during the collection, excavation, preparation, and taphonomic analysis of the fossil remains. The first half of this chapter concerns the methodology followed prior to the study described, which was established by various members of the scientific team responsible for the Malapa site and faunal material. If focuses on how the remains were collected at the site, how they were prepared, both physically and manually, and how they were catalogued. In the second half of the chapter, I describe the methods that I have used for the taphonomic study of the hominin remains. I chose a combination of classical taphonomic methods and modern CT scanning and 3D reconstruction techniques, in order to reconstruct the sequence of events that led to the preservation of MH1 and MH2, from death and decay to burial and recovery. This represents a new multidisciplinary approach that may be dubbed *palaeoforensic taphonomy*. It applies modern forensic methods of enquiry to the "cold case" of 1.977 million year old hominins in the same way taphonomy is applied to modern forensic cases, with the goal of understanding the causes of death and conditions surrounding burial. The traditional taphonomic methods used include a palaeontological approach, which looks at the context and the general characteristics of the faunal assemblage; a physical approach which, through a microscopic anlaysis, analyses bone surface modifications and identifies agents causing them; and a spatial approach, which for the first time, applies modern CT scanning and virtual technologies to reconstruct the original burial posture of the hominins into the deposit. Finally, I propose a definition of the new concept of *palaeoforensic taphonomy*, a discipline drawn from the fields of forensic anthropology, archaeology and taphonomy, before considering the various implications of burial and death postures in the palaeontological, archaeological and historical records, which form the core of this new concept and practice.

# 1. EXCAVATIONS, PREPARATION AND RECORDING

## 1.1. Excavation methods

Because the Malapa site underwent some limestone mining at the beginning of the 20th century (Dirks *et al*., 2010; Berger, 2012), the priority of the first field campaigns in 2008/2009 was to collect *ex situ* blocks that had been removed by the miners. These blocks were located on the surface, a few metres away from the main opening (Pit 1), mostly on the northern path that runs along the site. The *ex situ* blocks were taken to the Institute for Human Evolution (University of the Witwatersrand, Johannesburg) in order to be manually and/or virtually prepared.

During the first field season, some *in situ* remains were also collected from the deposit in Pits 1 and 2. These remains were of two types: some were recovered from decalcified sediment (Pit 1 and Pit 2) and therefore easily extractable using only a brush; others were embedded in the calcified sediment (only from Pit 1). The latter (mainly hominin remains) were removed, together with the calcified sediment that contained them, using a small axe for the small-sized blocks (J.M. Kibii, pers. comm.). In the case of the block containing MH2 bones, wedges, bars, as well as hydraulics were placed along natural cracks to free the block (L.R. Berger, pers. comm.). These blocks were later prepared in the laboratory. Systematic sieving of the excavated decalcified sediment was conducted using a 1 mm mesh-screen sieve (J.M. Kibii, pers. comm.).

A total station and laser theodolite (Nikon NPR 352) were set up in order to record the GPS coordinates of all the *in situ* remains and blocks containing bone specimens. The position of the *ex situ* blocks was also recorded. The X coordinate corresponds to the west-east position, the Y coordinate to the north-south position and the Z coordinate indicates the depth of the bones below the datum within the deposit. Figure 4.1 and Table 4.1 show the location in the site and the coordinates of the four points (Base, A1, B1 and C1) used as references during the setting up of the total station.

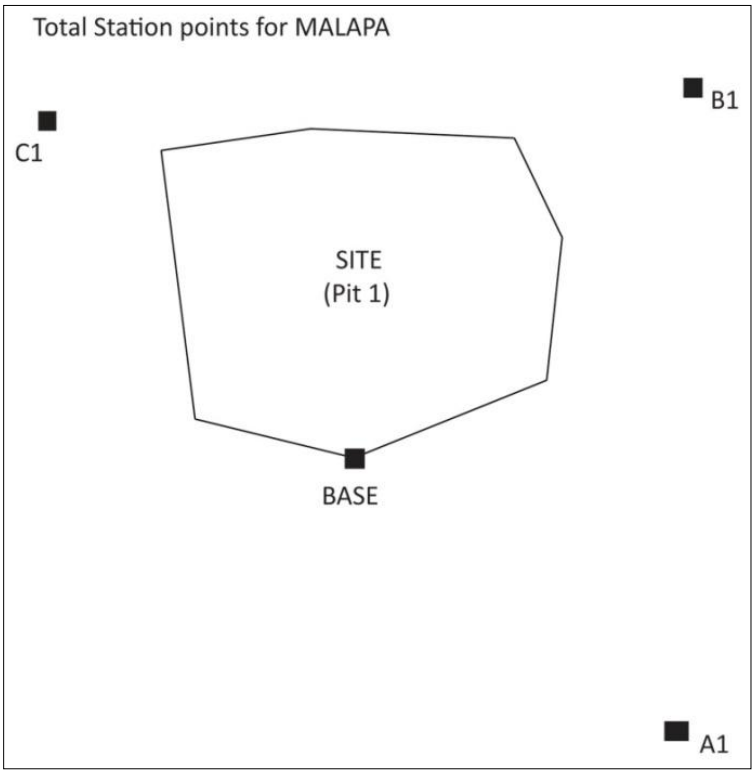



**Figure 4.1**. Position of the reference points used for the total station.

**Table 4.1**. X,Y and Z coordinates of the reference points.

| Point | East | North | Height |
|---|---|---|---|
| **BASE** | -80312.004 | 2865453.500 | 1417.200 |
| **A1** | -80320.233 | 2865464.176 | 1417.378 |
| **B1** | -80321.179 | 2865442.448 | 1415.389 |
| **C1** | -80295.765 | 2865446.855 | 1415.278 |

Two important points have to be borne in mind, as they have a great influence on the actual composition of the faunal assemblage. Firstly, the major part of the first field campaigns consisted of collecting all the blocks of calcified sediment removed by the miners and located around the pit, as well as fossils that were visible inside the deposits and present in loose decalcified sediment that did not require great investment in terms of excavations. The *in situ* deposits, together with the fossils they contain are therefore to date almost untouched. Secondly, priority was given to the recovery and collection of hominin remains, which means that the extremely high number of hominin remains present in the faunal assemblage might be, at least partly, explained by collectors bias.

This was true for both the *in situ* remains and the remains recovered from *ex situ* blocks. The order of preparation of blocks was organized according to their level of importance; with the ones containing potential hominin/primate remains first. CT scanning and virtual exploration techniques were applied to pre-identify possible hominin remains inside calcified blocks of sediment and prioritize the preparation of these blocks (see Smilg, 2012 and below).

### 1.2. Laboratory preparation methods

Acid preparation techniques using hydrochloric, acetic, and formic or thioglycollic acids to remove vertebrate fossil bones from calcified matrix were established almost a century ago and are still in use today (White, 1946; Toombs, 1948; Rixon, 1949; Toombs and Rixon, 1959; Rudner, 1972; Howie, 1974; Whybrow, 1985; Adams, 2006). Chemical preparation methods are usually preferred to physical methods due to the time investment, since manual removal of the matrix requires much more time than chemical dissolution. Chemical methods usually consist of solutions containing acid (concentration usually between 6 and 10%) dissolving the $CaCO_3$ component of the calcified sediment (Adams, 2006). However, acid preparation is a risky technique that, in some cases, can damage the fossils, produce cracks and render the bone surface friable (Toombs and Rixon, 1959; Rudner, 1972). Some authors recommend using it only on resistant bones and as a last resort because "there will always be some weakening of the bone when using acid, and the prepared specimen will be very fragile" (Rudner, 1972, p.121). In order to avoid any risk, and given the remarkable level of preservation of the bone surfaces of the Malapa fossils, it was decided to opt for physical preparation methods rather than chemical dissolution. The physical preparation is conducted under a microscope using an air-drill tipped with a small diamond head, allowing a high degree of precision during the removal of the calcified sediment. The physical preparation was conducted by the following people: C. Dube, S. Jirah, M. Kgasi, R. Languza, J. Malaza, G. Mokoma, P. Mukanela, T. Nemvhundi, M. Ngcamphalala, S. Tshabalala and C. Yates. In some cases, the

matrix was not removed completely, for instance when it was holding the bones together and/or because of potential preservation of organic material between the calcified sediment and the bones.

### 1.3. Virtual exploration of blocks of calcified sediment

Several hundreds of blocks were brought back from the site to the laboratory (Institute for Human Evolution, University of the Witwatersrand, Johannesburg). Given the time investment required by physical preparation, L.R. Berger and J.M. Kibii, the permit holders of the site, decided to apply Computed-Tomography (CT) scanning coupled with 3D exploration techniques, in order to conduct a preliminary sorting between blocks containing fossils and those with none, as well as to facilitate and guide manual preparation (see Smilg, 2012 for more details about the virtual preparation techniques applied at Malapa). One hundred and forty-two blocks were scanned at the Charlotte Maxeke Hospital of Johannesburg at the Radiography Service (co-supervised by J. Smilg and K.J. Carlson) using two CT-scanners, a Philips Brilliance 16 slice CT and a Siemens 40 slice CT; the protocol applied was a Head routine (Smilg, 2012).

The images obtained with the scanner were then processed using Avizo 6.2 computer software, in order to produce 3D volume renderings of the blocks (see below for more details about the virtual imaging techniques). For each block, the CT-scanner produces a stack of images or “Digital Imaging and Communication in Medicine” (DICOM) stack (one image every centimetre or every two centimetres). This stack of images is used by the Avizo software to produce an isosurface of the block, as well as an orthoslice, that allows accessing the internal part of the block. A virtual exploration of the blocks for fossil bones was subsequently conducted to preliminarily identify any bone, tooth and other fossil remains (e.g. coprolites, artifacts, insect pupae). Different variables, such as the size and geometry of the block, and the parametres chosen during the scan (e.g. field of view, section thickness and algorithms), affected the readability of the scanned images (Smilg, 2012). Depending on the quality of these data, it was in some cases possible to identify

the bones to Order (Primates, Artiodactyla, Perissodactyla or Carnivora). Each block was assigned a colour according to the level of priority for further physical preparation: red for "high priority" (blocks containing probable primate/hominin remains), white for "medium priority" (blocks containing non-primate identifiable faunal remains), and yellow for "low priority" (blocks containing non identifiable bone remains) (Smilg, 2012). Feedback was provided to the laboratory technicians concerning the location of the fossils within blocks and the types of fossil remains (when known) present inside blocks. This technique eliminated empty blocks from the physical preparation queue (see Smilg, 2012).

Identifiable fossils too small and/or fragile to be physically removed from the surrounding matrix were virtually extracted using Avizo. This was the case for a small mammal hemi-mandible (Val *et al*., 2011) and some hominin remains (e.g. MH1 skull, MH2 first rib, scapula, manubrium, and patella). For the hominin remains, renderings were used to generate a 3D printout.

### 1.4. Digital record of the excavation and preparation

Images were taken at each step of the excavation and fossil preparation processes, constituting a large database of several thousand digital and printed pictures. The preparation of blocks containing the hominin remains forms the large majority of the digital record, but pictures were also taken during the preparation of blocks containing non-hominin faunal remains. Numerous pictures taken during the collection of the blocks from the site are also on file.

### 1.5. Taxonomic attribution and cataloguing of the fossil remains

#### *1.5.1. Taxonomic identification*

Taxonomic attribution and anatomical identification were conducted by different members of the Malapa team studying hominin and non-hominin faunal material (L.R. Berger, J.M. Kibii, D.J. de Ruiter, B.F. Kuhn and C.M. Steininger).

### *1.5.2. Cataloguing of the faunal remains*

All faunal remains were given a catalogue number (prefix U.W. 88-...) consistent with the general indexing that was established by Zipfel and Berger (2009) for all fossils belonging or related in any way to the University of the Witwatersrand (housed in the collections of Wits and/or under the responsibility of someone linked to Wits). The number 88 refers to the Malapa site, which is the 88$^{th}$ site that falls under the responsibility of the University of the Witwatersrand (Zipfel and Berger, 2009). Information concerning the hominin and non-hominin faunal remains (specimen number, taxonomic and anatomical attribution) is entered in a Microsoft Access Database, and two separate Microsoft Word catalogues for the hominin and carnivore remains have also been established.

### *1.5.3. Creation of the database*

I have created a comprehensive Microsoft Excel Database that consists of 70 different fields for all the faunal material (hominin and non-hominin). In this database, information about the stratigraphic origin (*in situ*/*ex situ*, block and coordinates), taxon (family, genus and species) and anatomy (element, portion and side) is recorded, as well as about the type of bone breakage and surface modifications observed. For each field of information, I have used abbreviations commonly used by zooarchaeologists (Gifford and Crader, 1977; Costamagno, 1999a; see Appendix 3).

Eight anatomical regions have been defined in order to classify the different types of bones, inspired by the classification proposed by Fosse (1994) with some modifications (Table 4.2). The following bone categories are considered:

**Table 4.2.** Bone categories used in the database for faunal remains.

| BODY REGION | BONES |
|---|---|
| CRA (cranium) | calvarium, mandible and hyoid |
| TTH (teeth) | teeth |
| LBN (Long bones) | humeri, radii, ulnae, femurs, tibiae and fibulae |
| FBN (flat bones) | scapulae, pelvises |
| RACHIS | ribs, sternebrae, manubrium and clavicles |
| VER (vertebral column) | vertebrae and sacrum |
| META (metapodials) | metacarpals and metatarsals |
| SHBN (short bones) | carpals, tarsals, phalanges, patellae |

A complete list of abbreviations is provided in the explanation of the different fields of the database in Appendix 3.

## 2. CLASSICAL VERTEBRATE TAPHONOMY: THE TRIPLE APPROACH

### 2.1. Introduction

The first two approaches, namely palaeontological and physical, have been well described and used by researchers in the past decades. The "palaeontological approach", as described by Domínguez-Rodrigo *et al*. (2007), looks at the general aspects of the complete faunal assemblage and proposes interpretations based on the composition of the faunal spectrum, skeletal part representation and mortality profiles. The "physical approach" concerns the bone surface and "concentrates on changes in the physical attributes of bones throughout their taphonomic history" (Domínguez-Rodrigo *et al*., 2007, p.23). In other words, the physical approach aims at identifying all types of bone damage and the different agents that caused them, whether biotic or abiotic, based on modifications of the bone surface, both macro- and microscopically visible. I have chosen to use a third approach, the "spatial approach". Traditionally, the spatial approach is limited to the study of bone distribution in a deposit, and proceeds in two dimensions only (analysis of the bone distribution in the horizontal and vertical planes). Here, I combine new technologies (Computed-Tomography, micro-Computed-Tomography scanning methods and 3D rendering software) with more traditional techniques (study of orientation and direction of the bones in the deposit) to propose an innovative 3D model

of the spatial distribution of the hominin fossils within the deposit, and analyse its implications in terms of taphonomy of the assemblage (accumulation, site formation, fossilisation processes and original position of the hominin remains in the deposit).

## 2.2. Palaeontological approach

### *2.2.1. Quantitative units: definitions*

I refer to different quantitative units commonly used in zooarchaeology and taphonomy (Lyman, 1994a). These units serve to estimate the abundance of remains and identifiable specimens (NR, NISP and MNE), the number of individuals for each taxon (MNI) and to analyse the skeletal element representation and the degree of bone preservation (NR, NISP, MNE, MAU and percentage survival). A list of these units together with their definitions is provided below.

The total number of bone and tooth fragments recovered in the assemblage, including identified, identifiable and unidentifiable ones, is called **NR** (Number of Remains).

The **NISP** represents the total Number of Identified Specimens (Payne, 1975). The term "specimen" refers to any bone or tooth fragment identified to the anatomical level (Lyman, 1984) and/or the taxonomic level (Klein and Cruz-Uribe, 1984; Davis, 1987). The latter implies in most cases the former since taxonomic identification cannot be conducted without anatomical identification (Lyman, 1994b). Consequently, "identified" means a bone that was given either an anatomical and taxonomic attribution or only an anatomical attribution.

The **MNE** (Minimum Number of Elements; Bunn, 1982) is used to estimate the frequency of each skeletal element (Lyman, 1994b). In my estimation of the MNE, I have followed a manual overlap method as advocated by Bunn *et al*. (1986), taking into account criteria such as size and morphology. The criterion of age (infant, juvenile, adult, old) is also considered.

The **MNI**, or "Minimum Number of Individuals necessary to account for all the kinds of skeletal elements found in the skeleton of a taxon" (Lyman, 1994b, p.100), is calculated in order to estimate the abundance of different taxa within the assemblage (Plug and Plug, 1990). The MNI is estimated using the highest MNE value for each taxon and, as for the MNE, combines different criteria, such as age, size and morphology.

The **percentage survival** is used to calculate the degree of bone preservation in the faunal assemblage and to obtain information about body part frequencies. I refer to Brain's definition (1969, 1976), according to whom the percentage survival is the "observed proportion of each anatomical part that survived attritional processes" (Brain, 1969, 1976 in Lyman, 1994a, p.46). It is calculated as follows:

$$(100 \times MNE_e) / (MNI \times \text{number of times } _e \text{ occurs in one skeleton})$$

### *2.2.2. Fragmentation*

The intensity of bone fragmentation is informative in terms of the origin of the bone accumulation and diagenetic processes that have affected the bone assemblage (Binford, 1981; Brain, 1981; Lyman, 1994b). For instance, different carnivores (felids versus hyaenids) tend to produce different fragmentation ratios (Richardson, 1980) and several geological processes can lead to bone fragmentation (e.g. rockfalls, sedimentary compaction and movement; Brain, 1981; Texier, 2000). In order to estimate the degree of fragmentation, I compare two different ratios: the ratio complete/fragmentary bones and the ratio NISP/MNE (Richardson, 1980; Klein and Cruz-Uribe, 1984).

### *2.2.3. Breakage pattern*

It is possible to estimate whether a bone was broken while dry or fresh. This has taphonomic implications and can help the identification of the agent(s) responsible for the breakage of the bones (e.g. carnivores, percussion by a hammerstone, trampling or sedimentary pressure). Different studies have focused on describing green bone fractures (Myers *et al*., 1980; Binford, 1981; Bunn, 1981b, 1983; Haynes, 1983b; Johnson, 1985;

Lyman, 1987; Blumenschine, 1988; Blumenschine and Selvaggio, 1988) and different criteria have been proposed to describe the morphology of the breakage (Shipman *et al*., 1981; Villa and Mahieu, 1991). Here I refer to the criteria proposed by Villa and Mahieu (1991) for human long bones to differentiate between green and dry bone breakage patterns. Since these criteria have been established on long bones, I do not attribute a type of breakage to any other bone category. The fracture angle, outline and edge are considered, as well as the intensity of the fragmentation (i.e. shaft circumference, shaft fragmentation, lengths of the shaft fragments and breadth/length ratio). Fractures on dry bones are typically characterised by a right angle, a transverse outline and a jagged edge, whereas green bone fractures are associated with an oblique angle, curved outline and smooth edge (Villa and Mahieu, 1991).

### *2.2.4. Joints, articulations and disarticulation sequence*

A few definitions

The analysis of disarticulation pattern in a fossil assemblage can provide useful palaeoecological and taphonomic information, such as the length of time between death and burial, the impact and intensity of scavenging activities and the type of transport of the bones (Hill and Behrensmeyer, 1984; Smith, 1980, 1993). In forensic context, the degree of disarticulation can be influenced by the action of scavengers, such as canids, and can be used to estimate the postmortem interval (Haglund *et al*., 1989).

The term “articulation” refers to any direct contact in the body between two bones. Several articulations can form a “joint” such as the elbow joint, the hip joint or the knee joint, only to mention a few, which are themselves composed of several articulations. There are three different types of articulation, according to the type of movements they allow. The *diarthrosis*, or synovial articulation, is a mobile articulation that permits free movement, such as the articulations between the humerus and the scapula and between the femur and the pelvis. The *amphiarthrosis* is a semi-mobile articulation that allows limited movement and is connected with ligaments or elastic

cartilage (e.g. articulations between the vertebrae). The *synarthrosis* is an immobile articulation lacking a synovial cavity, which does not allow for any movement (e.g. articulations between the skull bones, also called sutures) (http://www.thefreedictionary.com).

In a natural environment, an undisturbed skeleton will normally disarticulate following a certain order, starting with the weakest joints and ending with the strongest ones (Table 4.3). The type of environment (dry versus wet) might modify slightly the sequence of passive disarticulation (see Hill, 1979a) but as a general rule, the resistance and strength of joints and articulations are related to the weight they are supporting (Duday, 2009). For instance, in humans, which are bipedal, the articulation between the skull and the mandible is weak, since it only supports the weight of the mandible, whereas the articulation between the sacrum and ilium is very resistant because it corresponds to the point where the lower body supports the weight of the upper body (Duday *et al*., 1990; Maureille and Sellier, 1996; Duday, 2009). The disarticulation order presents some variations between humans and quadruped mammals; they are presented here separately.

Persistent joints and articulations in the human skeleton

The persistent joints and articulations (Table 4.3) are the ones consistent with body parts subjected to high mechanical pressure, such as the atlas/occipital articulation, articulations between the lumbar vertebrae, between the sacrum and the last lumbar vertebra, the sacrum/ilium articulation, the femur/tibia articulation, and the joints of the ankles and tarsals (Duday *et al*., 1990; Maureille and Sellier, 1996). They mostly concern large-sized bones. Under undisturbed conditions, they can stay articulated for several months or even several years (Duday *et al*., 1990) and only disarticulate a long time after death and after decomposition (Maureille and Sellier, 1996). The articulations between the pelvic bone and the femur, and between the scapula and the humerus are called

"false persistent" articulations; they are in fact interlocking fragile articulations (see Adam *et al*., 1992 in Maureille and Sellier, 1996).

Unstable joints and articulations in the human skeleton

They concern fragile elements of the skeleton and/or small sized-elements (Table 4.3), such as the joints of the hands and the distal part of the feet (between metatarsals and phalanges), the articulations between the cervical vertebrae, the femur and the patella, the scapula and the thoracic cage, the ribs and the sternum and the temporal bone and the mandible (Duday *et al*., 1990, Maureille and Sellier, 1996; Duday, 2009). Under normal temperate conditions, it takes less than a few weeks for them to disarticulate (Duday *et al*., 1990; Duday, 2009).

**Table 4.3**. List of persistent, unstable and interlocking unstable joints and articulations in the human skeleton (after Duday *et al*., 1990; Maureille and Sellier, 1996; Duday, 2009).

| | |
|---|---|
| **Persistent** | occipital/atlas |
| | lumbar vertebrae |
| | last lumbar vertebra/sacrum |
| | sacrum/ilium |
| | femur/tibia |
| | distal tibia/calcaneum/talus (ankle joint) |
| | tarsals (calcaneum, talus, navicular) |
| **Unstable** | temporal bone/mandible |
| | cervical vertebrae |
| | hands (carpals, metacarpals and phalanges) |
| | distal part of the feet (metatarsals and phalanges) |
| | scapula/thoracic cage |
| | patella/femur |
| | sternum/ribs |
| | radius/ulna/humerus (elbow joint) |
| **Interlocking unstable** | pelvis (acetabulum)/femur |
| | scapula/humerus |

Disarticulation order in quadruped mammals

Different studies have been published regarding the disarticulation order in non-human quadruped mammals in various environmental conditions (Müller, 1951; Schäfer, 1962, 1972; Toots, 1975; Hill, 1979a, 1979b; Hill and Behrensmeyer, 1984; Andrews and Cook, 1985; Weigelt, 1989; Allison *et al.*, 1991). Undisturbed, the disarticulation is

complete after about five years (Hill and Behrensmeyer, 1984). The disarticulation pattern follows the same general order amongst the various species observed, even though some small differences have been noticed (Hill and Behrensmeyer, 1984). As an analogy for African conditions, I report here the results of observations conducted by Hill (1979a, 1979b) on Topi (*Damaliscus korrigum*) skeletons in the semi-desert region of east of Lake Turkana, in northern Kenya.

The first elements to disarticulate are the same as in humans (i.e. articulations consistent with low mechanical pressure and/or articulations not interlocking): scapula/rib cage articulation, caudal vertebrae, scapula/humerus articulation and mandible/temporal bone articulation (Figure 4.2). The more persistent articulations are the same as in the human disarticulation pattern: lumbar vertebrae/sacrum and vertebral column (Figure 4.2). The major difference concerns the cervical vertebrae that are unstable in the human skeleton whereas in herbivore skeletons they belong to the category of more resistant articulations. This might partly be due to the difference of mechanical pressure inflicted on the neck between biped and quadruped mammals.

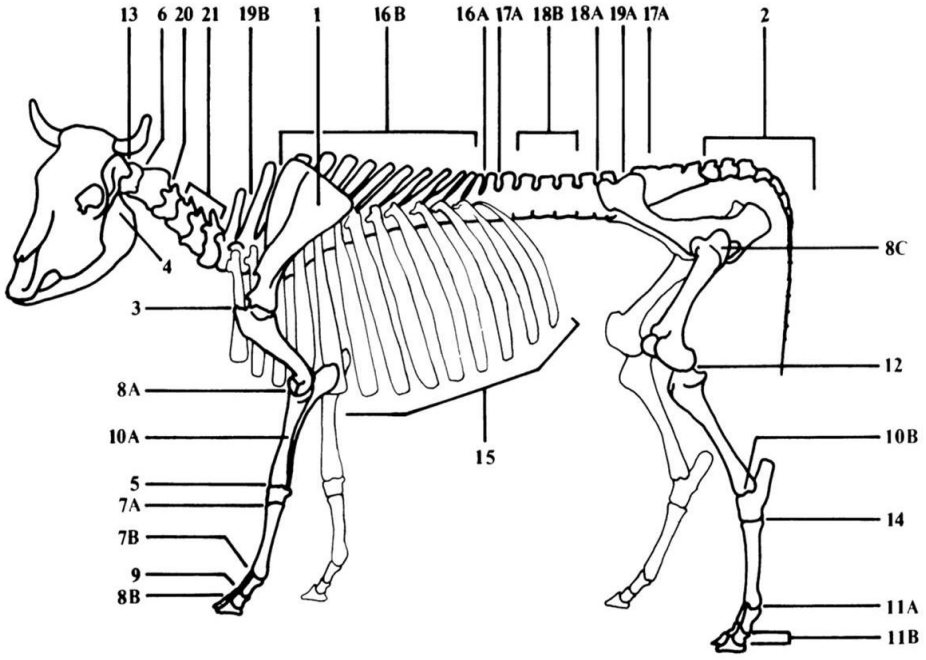



**Figure 4.2.** Disarticulation order observed amongst Topi carcasses, illustrated on a cow skeleton, from 1 (first elements to disarticulate) to 21 (last elements to disarticulate) (from Hill, 1979a).

Some observations conducted on disarticulation order of marine mammals (i.e. seals, dolphins and whales) show a similar pattern: again, the disarticulation starts around the extremities (mandible and skull, neck area and phalanges), whereas the vertebral column takes more time to disarticulate (Shäfer, 1972; Allison *et al.*, 1991).

The Malapa fossils: "true articulation" and "anatomical proximity"

I define two levels of articulation for the Malapa fossils: a "true articulation" refers to bones that are still directly associated with one another (direct contact, with no sediment between the bones), in their original anatomical position. The term "anatomical proximity" refers to bones that are articulated in the skeleton and preserved close to one another in the calcified sediment, but not fully articulated anymore. In other words, they are consistent with bones that are in anatomical position, with little displacement, but with some sediment infiltrated between the bones.

## 2.3. Physical approach

### *2.3.1. Introduction*

The different taphonomic agents that damage bones can be classified in two groups: biotic (e.g. mammalian and avian carnivores, hominin and non-hominin primates, suids and rodents) and abiotic agents (e.g. weathering, root etching, trampling, fluvial and sedimentary abrasion). These agents produce different types of damage on the bone surface. In Chapter 2, I have reviewed the different taphonomic agents present in southern African caves that could lead to bone accumulation and bone modification. In this chapter, I present a literature review on the taphonomic signature (characteristics of the bone damage) left by each of these agents.

### *2.3.2. Methods used for the analysis of bone surface modification*

The identification and the description of the bone surface modifications on the Malapa fossils was conducted using the naked eye as well as a systematic microscopic

analysis using an Olympus SZX 16 Multifocus microscope fitted with a digital camera at magnifications between 7 and 115 times. The only exception concerns two hominin remains (UW88-172, the manubrium of MH2 and UW88-198, the right first rib of MH2) considered too fragile to be removed from the matrix. A virtual extraction was conducted and the bone surface analysis made directly with 3D reconstruction software (Avizo 6.3) on the 3D rendering. A modern reference collection composed of various bones modified by a wide range of geological and biological agents, including hyaena, dog, leopard, cheetah, rodent, insect, river gravel, flood plain, trampling and stone tools, was also used.

### *2.3.3. Hominin damage*

Different stages of the butchery process (*sensu* Lyman, 1987a) conducted by hominins, including skinning, defleshing, bone breakage, marrow/brain extraction, cooking and consumption, can produce different types of bone modification, namely cut marks, percussion marks, tooth marks and burning. These types of modifications constitute clear and indisputable evidence of hominin action on a carcass (Binford, 1981; Lyman, 1994c). However, anthropogenic marks can be confused with modifications caused by other agents also contributing to the accumulation of the bone assemblage. Crocodiles (Njau and Blumenschine, 2006) and mammalian carnivores (Bonnischen 1973; Haynes 1980; Potts and Shipman 1981; Shipman and Rose, 1983a, 1983b; Eickhoff and Herrman, 1985; Cook, 1986; Blumenschine, 1988, 1995; Capaldo and Blumenschine, 1994; Oliver 1994; Selvaggio, 1994a, 1994b, 1998), as well as rodents (Pei, 1938; Binford, 1981; Potts and Shipman, 1981; Shipman and Rose, 1983; Cook, 1986), suids (Galdikas, 1978; Greenfield, 1988; Domínguez-Solera and Domínguez-Rodrigo, 2008) and chimpanzees (Pickering and Wallis, 1997; Tappen and Wanghram, 2000; Pobiner *et al*., 2007) can in some cases produce tooth marks that mimic anthropogenic cut marks, percussion and scrape marks. Trampling marks can also be confused with cut marks (Haynes and Stanford, 1984; Oliver 1984; Andrews, 1985; Behrensmeyer *et al*., 1986; Olsen and Shipman, 1988; Fiorillo, 1989; Nicholson, 1992; Domínguez-Rodrigo *et al*., 2009). Roots exploiting the

bone can leave furrows and grooves on the surface that can resemble anthropogenic stone tool marks (Binford, 1981; Shipman and Rose, 1983; Andrews and Cook, 1985; Cook, 1986). The natural bone surface morphology sometimes presents features that can be mistaken for cut marks (Binford, 1981; Morlan, 1984; Fischer, 1995; d'Errico and Villa, 1997; Mallye and Laroulandie, 2004). Finally, modern anthropogenic marks created during excavation, preparation and analysis of the fossils share some of the characteristics of ancient butchery marks, such as the V-shape cross section and the straight trajectory (Shipman, 1981; White and Toth, 1989).

Various studies have sought to establish criteria to distinguish between anthropogenic marks and other types of marks. These studies were motivated by two of the main questions tackled by palaeoanthropologists and zooarchaeologists: the emergence of meat acquisition and consumption in early hominin subsistence strategies (Bunn, 1981a; Crader, 1983; Bunn *et al*., 1986; Lupo, 1994; Selvaggio, 1994, 1998; Capaldo, 1995, 1997) and the practice of cannibalism by early humans (Trinkaus, 1985; Villa *et al*., 1986; White, 1986; Villa, 1992; Defleur *et al.*, 1999; Fernández-Jalvo *et al*., 1999; Pickering *et al*., 2000). Different criteria have been proposed to describe the exact morphology of cut marks and to distinguish them from other types of marks (Potts and Shipman, 1981; Shipman, 1981b; Shipman and Rose, 1983a, 1983b; Cook, 1986; Olsen and Shipman, 1988; Fiorillo, 1989). They were established using microscopic technology (optical microscope and scanning electron microscope). The criteria identifying anthropogenic cut marks are the following:

- the main groove presents a V-shaped cross section,
- the main groove has a straight trajectory,
- numerous micro-striations are present inside the cut mark, parallel to the main groove,
- the edges of the mark are parallel to each other,
- there is, in some cases, the occurrence of a "shoulder effect" (i.e. micro-striations forming on one or the two edges of the main groove),

- there is, in some cases, the occurrence of a “barb effect” (i.e. small group of micro-striations forming at the beginning and/or at the end of the main groove and running at a 45 degree angle opposite to the direction of the main groove).

Humans can also leave tooth marks on the bones during meat consumption (White, 1992). Recent studies describe human tooth marks produced experimentally (Saladié, 2009; Fernández-Jalvo and Andrews, 2011). Some ethnoarchaeological observations on tooth marks produced by modern hunter-gatherers on bones have also been published (Maguire *et al*., 1980; Andrews and Fernández-Jalvo, 1997; Landt, 2004, 2007; Martínez, 2009). Like other carnivores, humans can produce pits, punctures, notches, crenulated edges as well as shallow scores on the bones while chewing (Landt, 2007; Martínez, 2009; Saladié, 2009; Fernández-Jalvo and Andrews, 2011). Peeling, which is a type of fracture occurring on fresh bones chewed by human teeth, and characterised by “a roughened surface with parallel grooves or fibrous texture” (Fernández-Jalvo and Andrews, 2011), is also observed in the experimental (Fernández-Jalvo and Andrews, 2011) and fossil record (White, 1992). Based only on their size and morphology, tooth marks produced by humans are likely to be confused with those created by small carnivores such as jackals (Landt, 2007). Consequently, only a combination of contextual information about the deposit and occurrence of exclusively human teeth-inflicted types of damage such as “bent ends” (fraying), “curved shape at the very end of thin bones” and “double arch punctures on broken edges” (Fernández-Jalvo and Andrews, 2011) should allow the distinction between human and carnivore tooth marks.

### *2.3.4. Carnivore damage*

Carnivores of all sizes can potentially produce tooth marks on bones while feeding on animal carcasses, whether small carnivores such as foxes or badgers (Stallibrass, 1984; Castel, 1999; Mallye, 2007), medium-sized carnivores such as dogs, wolves, jackals, cheetahs and leopards (Haynes, 1980, 1983a; Brain, 1981; Morey and Klippel, 1991;

Selvaggio and Wilder, 2001; Domínguez-Rodrigo and Piqueras, 2003; Pickering *et al*., 2004c; Campmas and Beauval, 2008) or large carnivores such as lions and spotted hyaenas (Sutcliffe, 1970; Shipman and Phillips-Conroy, 1976, 1977; Binford, 1978, 1981; Maguire *et al*., 1980; Brain, 1981; Haynes, 1983a; Blumenschine, 1988, 1995; Blumenschine and Selvaggio, 1991; Capaldo and Blumenschine, 1994; Selvaggio, 1994a, 1994b, 1998; Capaldo, 1995; Andrews and Fernandez-Jalvo, 1997; Domínguez-Rodrigo, 1999; Selvaggio and Wilder, 2001; Domínguez-Rodrigo and Piqueras, 2003; Pickering *et al*., 2004b, 2004c; Pinto and Andrews, 2004; Domínguez-Rodrigo and Pickering, 2010). Different categories of bone modification have been observed, according to the location (on spongy versus compact bones) and the type of action performed by the carnivores. Table 4.4 provides a list of the different modifications produced by carnivores, together with their definitions.

**Table 4.4**. Different types of carnivore damage on bone.

| Category | Definition | References |
|---|---|---|
| **Pits** | Depressions with compact bone on the bottom, occurring as discrete, roughly circular markings, which scar the bone surface without any inward crushing of the bone cortex; they tend to have a localized distribution, typically adjacent to end chewing. | Maguire *et al*., 1980; Binford, 1981; Pickering and Wallis, 1997 |
| **Punctures (Tooth crushes)** | Depressions with spongy bone on the bottom; they are depressed, roughly circular holes produced by a carnivore tooth cusp, often a canine, which travels through the entire thickness of the bone's cortex and shows inward crushing. | Binford, 1981; Shipman, 1981a; Cook, 1986; Newman, 1993; Pickering and Wallis, 1997 |
| **Crenulated edge** | Surface of an edge removed by the teeth as an effect of intense punctures on very thin bone or ragged edge chewing, characterised by irregular jagged edges, which result from intense, sustained premolar/molar chewing. | Bonnischen, 1973; Shipman and Phillips-Conroy, 1976; Binford, 1981; Brain, 1981; Newman, 1993; Pickering and Wallis, 1997 |
| **Scores** | Parallel grooves resulting from the bone being turned or dragged against the teeth by the carnivore; with a length about three times longer than their width. They are produced by carnassials pressing on green bone and characterised by relatively shallow furrows, with smooth internal grooves that vary from V-shaped to U-shaped in cross-section depending on the morphology of the tooth cusp. | Haynes, 1980; Binford, 1981; Bunn, 1981; Potts and Shipman, 1981; Shipman, 1981a, 1989; Cook, 1986; Marshall, 1989; Newman, 1993; Selvaggio, 1994a; Blumenschine, 1995, 1996 |

| | | |
|---|---|---|
| **Furrows** | Grooves produced by the cusps of either the canines or the carnassials, as an effect of the repeated action of the jaw on cancellous bone. | Haynes, 1980; Binford, 1981 |
| **Scooping out** | Extreme result of furrowing. | Sutcliffe, 1970; Bonnischen, 1973; Binford, 1981 |
| **Digestion** | Polished aspect given to bone fragments that have been regurgitated by a carnivore. Attributes include widespread etching, erosion, perforation, smoothing, polish or thin edge termination and are most typically manifested as combinations of the above features on pieces less than 60 mm in length. Regurgitate bones are generally presented in two forms: the corroded, grossly striated form with thin sharp edges and perforations; and the rounded, more dense form which is smooth, polished and finely pitted. | Sutcliffe, 1970; Maguire *et al*., 1980; Behrensmeyer *et al*., 1989; Hill, 1989; Fisher, 1995; Villa and Bartram, 1996; d'Errico and Villa, 1997 |

### *2.3.5. Rodent damage*

Rodents were identified early on by zooarchaeologists as potential bone accumulation and modification agents. In forensic contexts, rodents such as rats and squirrels are known scavengers, which can feed on human cadavers in an advanced state of skeletonization, producing gnawing marks on bones and leading to scattering of bone remains (Haglund, 1992; Klippel and Synstelien, 2009). Amongst rodents, porcupine species (*Hystrix africaeaustralis, Hystrix cristata* and *Atherurus*) are well-known agents that accumulate and modify bones (Pei, 1938; Maguire *et al*., 1980; Binford, 1981; Brain, 1981; Shipman and Rose, 1983a; Cook, 1986). Porcupines tend to gnaw on dry and weathered rather than fresh bones, in order to wear down the incisors that grow throughout their life and not for nutritional reasons (Brain, 1981; Kibii, 2009). They produce parallel, "broad, contiguous shallow scrape marks" caused by the gnawing of the lower and upper incisors and "scooping or hollowing out of cancellous bone" (Maguire *et al*., 1980). Other rodents, such as brown rats, attack bones in the search of nutrients and preferably chew on the marrow-rich cancellous bone present on long bones extremities (Klippel and Synstelien, 2009). All rodents (e.g. squirrels, rats, mice) tend to produce the same types of marks in shape and morphology, owing to the fact that they gnaw bones in the same way, using their incisors. Only the size of the marks will differ from one species

to another (Binford, 1981; Shipman and Rose, 1983a; Cook, 1986). In some cases, rodent teeth can produce small parallel striations inside the main grooves (Shipman and Rose, 1983a). The repetition of the shallow scrape marks occurring next to each other forms what Shipman and Rose (1983a) call a "fan-shaped" pattern; this pattern is due to a specific way of chewing when the rodent uses its upper incisors as a pivot, and therefore scrapes repeatedly the bone surface with its lower incisors (Shipman and Rose, 1983a; Klippel and Synstelien, 2009). Another pattern has been described by the same authors and called "chaotic", consistent with a different type of gnawing where both the upper and lower incisors are drawn across the bone surface. This results in a "broad, depressed area traversed by many intersecting or overlapping marks" (Shipman and Rose, 1983a). Rodent tooth marks are "flat bottom U-shaped", which distinguishes them easily from carnivore tooth marks and human cut marks (Cook, 1986).

### *2.3.6. Other mammalian species damage*

Even though the literature is very scarce on this matter, a few studies have shown that other occasionally carnivorous mammals (e.g. omnivorous species such as primates and suids) can inflict damage to bones (Pickering and Wallis, 1997; Tappen and Wrangham, 2000; Pobiner *et al*., 2007, for the chimpanzees; Greenfield, 1988; Domínguez-Solera and Domínguez-Rodrigo, 2009, for the suids).

Chimpanzee damage to bone

Chimpanzees (*Pan troglodytes*) consume meat and can hunt small prey, including colobus monkeys, bushpigs and antelopes such as blue duikers and bushbucks, even though meat consumption represents only a small percentage of their diet (Kawabe, 1966; Teleki, 1973a, 1973b; Goodall, 1986; Boesch and Boesch, 1989; Uehara, 1997; Mitani and Watts, 1999, 2001; Boesch and Boesch-Achermann, 2000; Newton-Fisher *et al*., 2002; Pobiner *et al*., 2007). They can therefore accidentally leave chewing marks on the bone surface while feeding on carcasses. Experiments on captive chimpanzees feeding on bovid

and cervid bones show that they are capable of inflicting the "same range and degree of damage to bones as feeding carnivores" (Pickering and Wallis, 1997). These results were confirmed by observations on wild chimpanzees from the Kibale Forest in Uganda (Tappen and Wrangham, 2000; Pobiner *et al*., 2007). While chewing, chimpanzees can inflict pits, punctures, scores, notches and crenulated edges; they can produce peeling on the surface of cortical bone; they can also regurgitate and/or digest and consequently polish bone fragments (Pickering and Wallis, 1997; Tappen and Wrangham, 2000; Pobiner *et al*., 2007). Chimpanzee mastication damages are similar in shape and morphology to medium and large carnivore damage and both types can easily be confused, if based only on the analysis of bone surface modification (Pickering and Wallis, 1997; Tappen and Wrangham, 2000). Differences exist in terms of prey species, distribution of the damage on the skeleton, skeletal part frequencies in the scat assemblage, and degree of corrosion of the bones. Together with consideration of the context of the bone assemblage, these differences may allow researchers to distinguish between mammalian carnivore and chimpanzee damage (Pickering and Wallis, 1997; Tappen and Wrangham, 2000; Pobiner *et al*., 2007).

Suid damage to bone

Suids are omnivorous and feed on animal flesh when available, whether by scavenging on dead animal carcasses or by opportunistic hunting of weak prey such as young, old or ill individuals (Milstein, 1971; Cumming, 1975; Wilson, 1975; Grigson, 1982; Jones, 1984; Seydack, 1990; Herrero Cortés, 2001; Rosell *et al*., 2001). In Borneo, where Bornean bearded pigs (*Sus barbatus*) are well known to be very effective scavengers, a case of pigs feeding on ill/old orang-utans carcasses (found dead or killed by the pigs themselves) has been reported (Galdikas, 1976). Experimental studies and modern observations show that European pigs (domestic pigs, *Sus domesticus*, wild boars, *Sus scrofa* and hybrid boars) are very capable of producing bone damage similar in intensity to those inflicted by canids and hyaenids (Greenfield, 1988; Domínguez-Solera and

Domínguez-Rodrigo, 2009). They break long bones and create an assemblage with a high degree of fragmentation; they produce tooth marks in a similar fashion to carnivores (pits, punctures, scores and furrows). However, pigs tend to use their incisors much more prominently than carnivores, leading to the creation of scores and furrows different from carnivore-inflicted modifications. Pigs produce "long and flat tooth scores" and furrow the bones in a specific way by removing the spongy tissue horizontally. The tooth marks created are broad and shallow compared to carnivore tooth marks (Domínguez-Solera and Domínguez-Rodrigo, 2009).

No study has yet been carried out on the impact of African suids (bushpig, *Potamochoerus larvatus*, and common warthog, *Phacocheorus africanus*) on bones. Nevertheless, given the similarities in diet and behaviour between the different suid species, it is reasonable to argue that results obtained on Eurasian pigs can be applied to their African cousins, considering that African species are also omnivorous, can feed on animal carrion and hunt small prey in some cases (Milstein, 1971; Cumming, 1975; Wilson, 1975; Jones, 1984; Seydack, 1990; Skinner and Chimimba, 2005).

### *2.3.7. Bird of prey damage*

Birds of prey consume at least parts of micro, small and medium-sized mammals and can produce different types of damage whether during the capture, consumption or digestion of the carcass (Brain, 1981; Andrews, 1990; Sanders *et al*., 2003; McGraw *et al*., 2006; Trapani *et al*., 2006). Different extant species of birds of prey (see Table 4.5), namely owls (Brain, 1981; Andrews, 1990), various species of eagles (Andrews, 1990; Berger and Clarke, 1995; Berger, 2006) and vultures (Andrews, 1990; Robert and Vigne, 2002a, 2002b; Costamagno *et al*., 2008; Marín Arroyo *et al*., 2009) have been identified as bone accumulation and modification agents in modern and fossil assemblages. Actualistic observations (Andrews, 1990 for owls, eagles and vultures; Robert and Vigne, 2002a, 2002b for the bearded vultures; Sanders *et al*., 2003; McGraw *et al*., 2006; Trapani *et al*.,

2006 for eagles) have allowed the description of their taphonomic signature on bone remains, which can be distinguished from other types of predators.

**Table 4.5**. Birds of prey for which information exist in terms of bone accumulation and damage.

| Family | Common name | Scientific name | Geographical location | Reference |
|---|---|---|---|---|
| **STRIGIDAE** | Spotted eagle owl | *Bubo africanus* | Europe, Africa | Brain, 1981; Andrews, 1990 |
| | Cape eagle owl | *Bubo capensis* | Africa | Brain, 1981 |
| | Giant eagle owl or Verreaux eagle owl | *Bubo lacteus* | Africa | Brain, 1981; Andrews, 1990 |
| | Barn owl | *Tyto alba* | Europe, Africa | Brain, 1981; Andrews, 1990 |
| | Snowy owl | *Bubo scandiacus* | Europe, Asia, North America | Andrews, 1990 |
| | Long-eared owl | *Asio otus* | Europe, Asia, North America | Andrews, 1990 |
| | European eagle owl | *Bubo bubo* | Europe, Asia | Andrews, 1990 |
| | Great grey owl | *Strix nebulosa* | Asia, North America | Andrews, 1990 |
| | Tawny owl | *Strix aluco* | Europe, Asia | Andrews, 1990 |
| | Little owl | *Athena noctua* | Europe | Andrews, 1990 |
| | Short-eared owl | *Asio flammeus* | Europe | Andrews, 1990 |
| **FALCONIDAE** | Kestrel | *Falco tinnunculus* | Europe, Asia, North Africa | Andrews, 1990 |
| | Peregrine | *Falco peregrinus* | All continents | Andrews, 1990 |
| | Gyrfalcon | *Falco rusticolus* | Europe, Asia, North America | Andrews, 1990 |
| **PANDIONIDAE** | Osprey | *Pandion haliaetus* | Europe, Asia, Africa, America | Andrews, 1990 |
| **STERCORARIIDAE** | Arctic skua | *Stercorarius parasiticus* | Europe, Asia, North America | Andrews, 1990 |
| **ACCIPITRIDAE** | Crowned hawk-eagle | *Stephanoaetus coronatus* | Africa | Andrews, 1990 ; Sanders *et al.*, 2003 ; Berger, 2006 ; McGraw *et al.*, 2006 ; Trapani *et al.*, 2006 |
| | Verreaux's eagle or black eagle | *Aquila verreauxii* | Africa | Berger and Clarke, 1995 |
| | Bonelli's eagle | *Aquila fasciata* | Europe, Asia, Africa | Andrews, 1990 |
| | Martial eagle | *Polemaetus bellicosus* | Africa | Andrews, 1990 |
| | Hen harrier | *Circus cyaneus* | Europe, Asia, North America | Andrews, 1990 |
| | Common buzzard | *Buteo buteo* | Europe, Asia | Andrews, 1990 |
| | Red kite | Milvus milvus | Europe | Andrews, 1990 |
| | Bearded vulture | *Gypaetus barbatus* | Europe | Robert and Vigne, 2002a, 2002b |
| | White headed vulture | *Trigonoceps occipitalis* | Africa | Andrews, 1990 |
| | Griffon vulture | *Gyps fulvus* | | Domínguez-Solera & Domínguez-Rodrigo, 2011 |
| **CATHARTIDAE** | Andean condor | *Vultur gryphus* | South America | Andrews, 1990 |

In terms of bone surface modification, two categories can be distinguished: digestion marks due to gastric acid of the bird stomach and punctures/scores due to the action of beak and talons.

Owls tend to take prey smaller than themselves and consume them without dismembering them. They produce less breakage than diurnal birds (e.g. falcons, buzzards, eagles) (Andrews, 1990), even though Brain (1981) mentions a particular destruction pattern of the nasal and the calvaria of small mammals caused by the Cape eagle owl. The main type of damage caused by owls seems to be digestion marks due to the action of the gastric acid on bones regurgitated in a pellet (Andrews, 1990).

Diurnal birds on the other hand can take bigger prey and dismember the carcass during consumption (Andrews, 1990), producing marks on the bones. Several studies have looked at bone damage caused by the Crowned hawk-eagle (*Stephanoaetus coronatus*) on monkey skeletons (Berger and Clarke, 1995; Sanders *et al*., 2003; Berger, 2006; McGraw *et al*., 2006; Trapani *et al*., 2006; Berger and McGraw, 2007). The action of the beak and talons during the feeding process produces modifications occurring predominantly on thin bones such as skulls and innominates (i.e. “can-opener” perforations producing bony flap, punctures and nicks on the pelvis and the cranium, especially around the orbits, maxillae, sphenoid and parietals). It also causes the scapulae to be very raked and shattered as a result of the bird opening the thoracic cavity to extract the heart and lungs. The long bones usually remain intact or show only a few punctures (Sanders *et al*., 2003; McGraw *et al*., 2006; Trapani *et al*., 2006).

The only observations on bone damage inflicted by vultures have been conducted on European species (i.e. *Gypaetus barbatus* and *Gyps fulvus*) (Robert and Vigne, 2002a, 2002b; Domínguez-Solera and Domínguez-Rodrigo, 2011). These species modify bones in the form of digestion marks due to gastric acid (Robert and Vigne, 2002a, 2002b), shallow scores, punctures and “roughly circular to oval pits” produced on all anatomical parts

except radio-ulnae, phalanges, metapodials and carpals (Domínguez-Solera and Domínguez-Rodrigo, 2011).

### *2.3.8. Insect damage*

Introduction

Though insect damage on fossil bones from Pleistocene assemblages is not described as being commonly preserved or recognized and rarely described in the literature (Tobien, 1965; Kitching, 1980; Martin and West, 1995; Dominato *et al*., 2009; Huchet *et al*., 2011; Pomi and Tonni, 2011; Backwell *et al*., 2012), compared to other biotic agents, such as mammalian carnivores, rodents and birds of prey, the impact of insects on carcasses is well known by forensic anthropologists (Derry, 1911; Byrd and Castner, 2010; Huchet *et al*., 2011), as well as in museum preparation, where insects and especially dermestid beetles are used to clean skeletons (Hefti *et al*., 1980; Weichbrod, 1987). Insect damage on the bones of dinosaurs (Hasiotis *et al*., 1999; Roberts *et al*., 2002; Hasiotis, 2004; Britt *et al*., 2008; Bader *et al*., 2009; Saneyoshi *et al*., 2011), Oligocene (Fejfar and Kaiser, 2005), Miocene (Tobien, 1965) and Pliocene mammals (Martin and West, 1995; Kaiser, 2000; Kaiser and Katterwe, 2001) has been abundantly described in the literature and used for taphonomic inferences. A large variety of insects feed on carrion, from the beginning to the end of the decomposition process (Bornemissza, 1957; Payne, 1965; Payne and King, 1970, 1972; Thorne and Kimsey, 1983; Smith, 1986; Weigelt, 1989; Byrd and Castner, 2010). Forensic entomologists have extensively studied the successive colonization by various insect species on a corpse. It follows a specific order and depends on environmental and external conditions well described in the literature (Payne *et al*., 1968; Payne and King, 1972; Leclerc, 1978; Rodriguez and Bass, 1985; Smith, 1986; Weigelt, 1989; Kulshresta and Satpathy, 2001; Marchenko, 2001; Amendt *et al*., 2004; Byrd and Castner, 2010). In forensic anthropology, the identification and analysis of insect damage allows the calculation of the postmortem interval (PMI) and provides information concerning the conditions of the death and, if it is the case, of the burial (Kulshresta and

Satpathy, 2001; Marchenko, 2001; Amendt *et al*., 2004; Byrd and Castner, 2010; Huchet *et al*., 2011). In archaeology and palaeontology, the identification of insect damage on fossil bones, together with the identification of the insect species responsible for the damage, can provide interesting ecological, climatic (e.g. temperature and humidity conditions during the decomposition process) and taphonomic data (e.g. presence/absence of carnivore scavenging, timing of death and burial processes, state of the carcass when the insect fed on it, season of death) (Martin and West, 1995; Hasiotis *et al*., 1999; West and Martin, 2002; Britt *et al*., 2008; Bader *et al*., 2009; Saneyoshi *et al*., 2011).

Species that modify bones

Several insect families belonging to three distinct groups have been identified as modifying agents of bone and horn corn surfaces: termites (Termitidae, Mastotermitidae and Rhinotermitidae) (Derry, 1911; Behrensmeyer, 1978; Watson and Abbey, 1986; Kaiser, 2000; Kaiser and Katterwe, 2001; Huchet *et al*., 2011; Pomi and Tonni, 2011; Backwell *et al*., 2012), beetles (Dermestidae, Tenebrionidae and Scarabaeoidae) (Tobien, 1965; Hefti *et al*., 1980; Kitching, 1980; Martin and West, 1995; Hasiotis *et al*., 1999; Hasiotis, 2004; Roberts *et al*., 2007; Britt *et al*., 2008; Bader *et al*., 2009; Dominato *et al*., 2009) and moths (Tineidae) (Behrensmeyer, 1978; Hill, 1987).

Types of damage

The description of bone damage caused by insects and the attribution of this damage to a specific insect group is in most cases based on the observation of fossil and modern bones bearing marks interpreted as insect damage (Behrensmeyer, 1978; Kitching, 1980; Hill, 1987; Martin and West, 1995; Hasiotis *et al*., 1999; Kaiser, 2000; Hasiotis, 2004; Fejfar and Kaiser, 2005; Britt *et al*., 2008; Bader *et al*., 2009; Dominato *et al*., 2009; Pomi and Tonni, 2011), combined with actualistic inferences about the behaviour of extant insect species. Experimental studies have permitted a more accurate

description of the types of bone damage caused by termites (Watson and Abbey, 1986; Backwell *et al*., 2012) and dermestid beetles (West and Hasiotis, 2007).

Two separate causes leading to bone surface modification are distinguished in the literature. The first type of modification is due to the habit of some insects to bore their pupation chambers into the bone surface. This has only been mentioned for beetles (Order Coleoptera) and especially dermestid beetles (Tobien, 1965; Kitching, 1980; Hasiotis *et al*., 1999; Hasiotis, 2004; Roberts *et al*., 2007; Bader *et al*., 2009; Dominato *et al*., 2009). The pupating structures (pupation chambers *per se* and associated borings) are excavated by adults using their mandibles (Martin and West, 1995). The dimensions of the pupation chambers are consistent with the size of the larvae. Table 4.6 regroups the different characteristics of marks observed on fossil bones associated with dermestid beetle pupation activities.

**Table 4.6**. Description of insect damage associated with pupation chambers of dermestid beetles.

| Description of the modification | Reference |
|---|---|
| "holes and burrows" penetrating into the shaft of long bones (4-5 mm and sometimes even into the marrow cavity) | Kitching, 1980 |
| "circular to elliptical-shaped borings" from 0.5 to 5.0 mm in diameter and that do not penetrate deeply the bone surface | Hasiotis *et al*., 1999 |
| "hollow, oval chambers with concave flanks bored into inner spongy and outer cortical bone surfaces" | Roberts *et al*., 2007 |
| "circular to elliptical borings" | Hasiotis, 2004 |
| shallow pits, rosettes and hemispherical pits | Bader *et al*., 2009 |
| "hollow oval-shaped structures (without filling) excavated in the spongy bone" | Dominato *et al*., 2009 |

Another type of modification is caused by the action of feeding on the carcass/bones by insects. It can be insects feeding either on the bone itself or on dry matter left on the carcass such as skin, ligaments and tendons. Because the insects are using their mandible for this purpose, the shape and morphology of the traces are consistent with the shape and morphology of the insect mandibles. Different marks on bones produced by insect mandibles have been described. Termites produce scratches (Watson and Abbey, 1986; Fejfar and Kaiser, 2005; Pomi and Tonni, 2011), shallow grooves with a U-shaped profile (Kaiser, 2000; Kaiser and Katterwe, 2001), star-shaped

pits and grooves showing a radial morphology and sometimes present in clusters (Kaiser, 2000; Fejfar and Kaiser, 2005; Pomi and Tonni, 2011). Huchet *et al*. (2011) have observed sub-cortical cavities, superficial pits, bores, large furrows and sub-circular perforations in human bones attacked by termites. In a recent experiment, Backwell and colleagues (2012) illustrate eight types of damage produced by termites (*Trinervitermes trinervoides*) on bones: destruction of the bone, bore holes, etched surface texture, surface pits, star-shaped marks, cluster of sub-parallel striations, parallel striations and the presence of surface residue. Beetles produce "shallow, meandering surface trails, composed of actuate grooves or scratches, bored into compact bones surfaces" (Roberts *et al*., 2007, p.201) as well as elliptical to round pits occurring in clusters and shallow bores, both occurring on cortical bone, opposite sets of parallel grooves, bores penetrating deep into the bone (in some cases leading to the destruction of the bone) and sinuous furrows located on articular surfaces (Britt *et al*., 2008). The damage caused by moths is produced by the larvae feeding on the organic components of the carcass and have been described as grooving marks (Behrensmeyer, 1978).

Invertebrate damage to bones: experimental approach

Research in progress by Backwell and colleagues, including myself, concerns controlled experiments with a number of arthropods and molluscs, selected on the basis of their mouth parts, and in the case of *Achatina* land snails and millipedes, because they are present in the Malapa fossil assemblage. Table 4.7 lists the various invertebrate taxa involved in the laboratory experiment. Each taxon was offered a range of bone types (spongy, compact, thick and thin cortical) in different states of preservation (fresh, dry, fossil) for the duration of one summer season, when they are all active.

**Table 4.7**. List of insects and gastropods used in the experiment.

| **Common name** | Parktown prawn (male) | Toktokkie | Trogidae hide beetle |
|---|---|---|---|
| **Phylum** | Arthropoda | Arthropoda | Arthropoda |
| **Class** | Insecta | Insecta | Insecta |
| **Order** | Orthoptera | Coleoptera | Coleoptera |
| **Family** | Anostostomatidae | Tenebrionidae | Trogidae |
| **Genus** | *Libanasidus* | - | *Omorgus* |
| **Species** | *vittatus* | - | *squalidus* |
| **Number of animals** | 2 | 20 | 5 |

| **Common name** | Woodlice | Millipede large | Garden snail | Achatina |
|---|---|---|---|---|
| **Phylum** | Arthropoda | Arthropoda | Mollusca | Mollusca |
| **Class** | Malacostraca | Diplopoda | Gastropoda | Gastropoda |
| **Order** | Isopoda | - | - | - |
| **Family** | - | - | Helicidae | Achatinidae |
| **Genus** | - | *Archispirostreptus* | *Helix* | *Achatina* |
| **Species** | - | *gigas* | *aspersa* | - |
| **Number of animals** | - | 10 | 20 | 3 |

### *2.3.9. Trampling*

Sedimentary abrasion of bone surface, breakage and dispersion of bones due to animal (including human) trampling has been identified and described as a potential biotic taphonomic process in palaeontological and archaeological assemblages (Brain, 1967; Myers *et al*., 1980; Agenbroad, 1984; Fiorillo, 1984; Oliver, 1984, 1986; Behrensmeyer *et al*., 1986). The effects of trampling have been well studied experimentally (Andrews and Cook, 1985; Behrensmeyer *et al*., 1986; Domínguez-Rodrigo *et al*., 2009). Trample marks can be defined as "shallow, sub-parallel sets of scratch marks" (Fiorillo, 1984, p.47); they present a V-shape or a rounded basal cross-section with the outer edges generally rounded, with sometimes an internal grooving in experimentally-produced marks (Behrensemeyer *et al*., 1986). Trample marks can easily be differentiated from rodent and carnivore tooth marks (Fiorillo, 1984; Andrews and Cook, 1985), but their distinction from anthropogenic butchery marks can be difficult (Andrews and Cook, 1985; Behrensmeyer *et al*., 1986; Olsen and Shipman, 1988; Domínguez-Rodrigo *et al*., 2009). The consideration of other criteria (e.g. frequency of the marks, orientation on the bones, location on the skeleton, and general context of the bone assemblage) can permit the differentiation

between trample and butchery marks (Andrews and Cook, 1985; Behrensmeyer *et al*., 1986; Domínguez-Rodrigo *et al*., 2009).

*2.3.10. Damage caused by abiotic agents*

Weathering

Weathering refers to the chemical and mechanical deterioration of animal carcasses, due to environmental factors (e.g. temperature, humidity level, sunlight). Together with a global understanding of the taphonomic and geological context, the evaluation of the degree of weathering affecting a fossil assemblage can provide important information concerning the local environmental conditions in which the animals have decomposed and, in some cases, the time of exposure of the bones (between death and burial) (Behrensmeyer, 1978; Lyman and Fox, 1989). For the analysis of the Malapa faunal assemblage, I refer to the last five stages of weathering established by Behrensmeyer (1978), from 1 to 5 (stage 0 is consistent with fresh bones and therefore never occurring in a fossil assemblage). Table 4.8 summarises the characteristics for each weathering stage.

**Table 4.8**. Different weathering stages affecting bones (from Behrensmeyer, 1978).

| Stage | Characteristics |
|---|---|
| **0** | The bone is fresh and usually greasy with some soft tissue (skin, flesh, marrow) still preserved; there is no sign of cracking or flaking. |
| **1** | Cracks start appearing; some soft tissue can still be present. |
| **2** | The flaking begins on the outermost surface of the bone; some tissue can still be present (but not always). |
| **3** | The external part of the bone is removed; the presence of rough patches of weathered bone can be noticed; there is usually no tissue preserved at this stage. |
| **4** | The bone surface is coarsely fibrous; the cracks are open; occurrence of large and small splinters that can fall away from the main bone. |
| **5** | The bone is completely falling apart as a result of the intense flaking. |

Root etching

In some cases, roots can attack the bone surface, producing a complex network of "thin, curvilinear branched grooves" with a U-shaped cross section and sometimes linear

arrangements of pits (Binford, 1981; Bader *et al*., 2009, p.140). The damage is due to roots and rootlets growing on the bone surface and secreting acids that dissolve the bone matrix (Shipman, 1981b). The observation of root etching on fossils can provide information about the context in which the bones were preserved, namely the presence of vegetation in the vicinity (Shipman, 1981b).

Water abrasion

In the case of isolated bones transported by flowing water, the abrasion due to impacts by sediment load contained in the water promotes rounding and polishing of the bone surface (Shipman and Rose, 1988; Fernández-Jalvo and Andrews, 2003) and can remove it altogether. Water abrasion can in some cases obliterate the detailed morphology of the bone surface, erasing previous modifications such as cut marks (Shipman and Rose, 1988). The "abrasion of compact bone may open up vascular channels lying just beneath the surface and push fragments of bone into them" (Shipman, 1981b, p.381). Experimental study on the effect of water abrasion on bones show that the type of sediment (coarse versus fine) present in the water, as well as the weathering stage of bones (fresh, dry, weathered or fossil), influence the degree of abrasion. The fossil bones (from a Middle Pleistocene cave deposit in Fernández-Jalvo and Andrews's experiment; no precision concerning the stage of fossilization in Shipman and Rose's experiment) are more rapidly and more intensively damaged than the other types of bones; and the coarser the sediment is, the more intensive the degree of abrasion (Shipman and Rose, 1988; Fernández-Jalvo and Andrews, 2003).

## 2.4. Spatial approach

### *2.4.1. Introduction: background*

Analysing the distribution of bone remains in a palaeontological or archaeological site provides useful information in terms of site formation process and taphonomic agents that have affected the assemblage (Rigaud and Simek, 1991; Smith, 1993; Lyman, 1994b;

Marean and Bertino, 1994; Nigro *et al*., 2003; Jennings *et al*., 2006; Mallye, 2007, 2011). In palaeontological assemblages, fluvial dispersal can be identified based on the way bones are concentrated, distributed and orientated in the deposit (Voorhies, 1966, 1969; Behrensmeyer, 1975, 1982; Boaz and Behrensmeyer, 1976; Hanson, 1980; Smith, 1980, 1993; Boaz, 1994). Spatial data help the identification of perturbations due to biological agents such as carnivores, which can cause significant bone dispersal while feeding on carcasses (Brain, 1981; Binford *et al*., 1988; Marean and Spencer, 1991; Stiner, 1991; Lyman, 1994; Marean *et al*., 1992; Marean and Bertino, 1994; Kjorlien *et al*., 2009), as well as burrowing animals, such as badgers and earthworms, which can modify the spatial arrangement of bone remains in a deposit (Wood and Johnson, 1978; Armour-Chelu, 1994; Mallye, 2007, 2011). Conducting a spatial analysis requires that the X-Y-Z coordinates of the remains were recorded, which is not always the case with assemblages that were excavated a long time ago. Hence, only a few studies (Nigro *et al.*, 2003; Jennings and Hasiotis, 2006; Mallye, 2011) have applied spatial analysis, namely Geographical Information System (GIS), to a palaeontological/archaeological assemblage in order to understand its taphonomic history and the formation process of the site. Spatial analyses have mostly been conducted in 2D, but the development of a 3D extension to the Arc View GIS software allows researchers to now conduct their spatial analysis in three dimensions (Nigro *et al*., 2003; Jennings and Hasiotis, 2006).

### *2.4.2. Medical CT and microfocus CT scanning of hominin bones*

<u>General introduction: principles and applications of the method</u>

Medical Computed-Tomography (CT) and microfocus CT scanning methods, coupled with 3D rendering software (e.g. AMIRA, Avizo, VG Studio Max, Treatment and Increased Vision for Medical Imaging or TIVMI) constitute very powerful non-invasive tools for the analysis of fossils. They have been increasingly used by palaeontologists and palaeoanthropologists in the past two decades for a large range of purposes (Zollikofer *et al*., 1998; Zollikofer and Marcia Ponce de León, 2005). Once original fossils have been

scanned, these technologies allow accurate qualitative and quantitative studies on 3D replicas without any risk of damaging the originals (Zollikofer *et al*., 1998; Zollikofer and Marcia Ponce de León, 2005). Figure 4.3 presents a flow diagram that illustrates the principles and applications of computer-assisted technology to the fossil record.

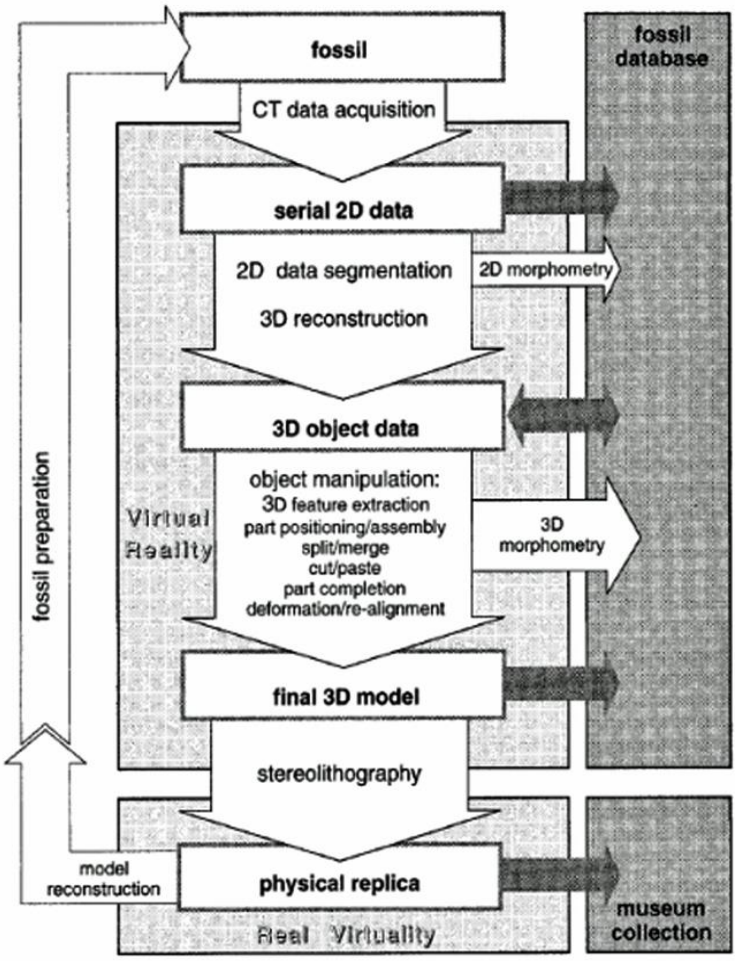



**Figure 4.3**. Principles of computer-assisted technology applied to palaeontology and palaeoanthropology (from Zollikofer *et al*., 1998).

Combining computed tomography and 3D reconstruction techniques offers the possibility to virtually restore the original shape and morphology of fossil specimens that have been distorted (e.g. because of sedimentary pressure), as well as to reconstruct fragmentary fossil specimens (Zollikofer *et al*., 1998, 2005; Wu and Schepartz, 2009). The combined technologies also permit (1) virtual and non-invasive exploration of internal parts of a fossil that are invisible on the original specimens and/or (2) virtual preparation

of a fossil still embedded within surrounding matrix (Conroy and Vannier, 1984; Wind, 1984; Luo and Ketten, 1991; Maisey, 2001; Zollikofer *et al*., 2002; Zollikofer and Marcia Ponce de León, 2005; Lordkipanidze *et al*., 2006; Wu and Schepartz, 2009; Carlson *et al*., 2011; Val *et al*., 2011). Computed Tomography technology has been applied to bone density research (Lam *et al*., 1998; Carlson and Pickering, 2003; Novecosky and Popkin, 2005), morphometric (Guyomarc'h *et al*., 2012), biomechanical (Zollikofer and Marcia Ponce de León, 2005), and age estimation studies (Colombo *et al*., 2012). 3D printouts produced from 3D renderings can be used as near-identical replicas of the original fossil for future studies and/or distributed to museums, universities, and so on. This prevents excessive handling of original fossils and also provides a way of producing replicas that does not involve, as the classic casting methods do, risking damaging surfaces of original specimens.

Scanning of the Malapa remains

The MH1 skull, together with most post-cranial elements of the same individual (i.e. elements of the pelvis and long bones), were scanned in Grenoble, France, using synchrotron technology, at the European Synchrotron Radiation Facilities (ESRF), under the direction of L.R. Berger, K.J. Carlson and P. Tafforeau (Carlson *et al*., 2011). Other specimens were scanned at the Charlotte Maxeke Hospital in collaboration with J. Smilg using a medical CT-scanner. I have CT-scanned the replicas rather than the original bones. The 3D renderings produced from scan data of the casts are not as good as renderings produced from scan data obtained from original fossils, but they are sufficient for inclusion in illustrations of geospatial results, which do not aim at providing any detailed morphological or morphometric description of the bones, but to discuss the spatial distribution of the fossils.

### *2.4.3. 3D renderings of hominin remains produced using Avizo software*

Introducing the Avizo software

The creation of 3D renderings of hominin remains was conducted using Avizo (version 6.2 at the beginning of the project, but upgrades permitted use of version 6.3 later on). Avizo is a commercial visualization software package developed by Visualization Sciences Group (www.vsg3D.com). It permits visualizing, processing and analyzing any kind of 3D data, for industrial and scientific purposes.

Creation of 3D renderings

Both the microfocus CT and medical CT scanners produce a stack of .tiff files for each bone or group of bones that is scanned. This stack of images is then processed in Avizo, creating an isosurface of the bone, or 3D surface rendering, which is subsequently saved as a .surf or .stl formatted file. K.J. Carlson produced 3D renderings of original fossils, scanned whether using medical CT or microfocus CT image data. I created 3D renderings of the bones for which only the casts were scanned.

### *2.4.4. Direction and inclination*

Definitions

The direction considers the general orientation of the bones as well as the way the specimen is aligned (i.e. which cardinal point the proximal part is facing and which cardinal point the distal part is facing). For this matter, I only consider bones with a length longer than the width (i.e. long bones, some flat bone fragments, phalanges, ribs and mandibles).

The inclination of the bone refers to the angle of the main axis of a specimen relative to the horizontal, inside the deposit.

Combining these two aspects indicates whether there is a particular orientation and distribution of the bones within the different facies.

Estimation of the direction and inclination of the fossils

Two types of estimation, depending on whether or not the stratigraphic origin of the blocks was known, were conducted.

For the remains in blocks of known origin or still *in situ*, I have considered the direction of the remains within a geographical plane (north, south, east and west). In the lab, for the remains for which the exact position in the deposit is known (i.e. all the bones from the MH2 arm block), virtual measurements were taken on the 3D renderings of the blocks using the Avizo 6.3 software, which allows measuring distances and angles.

For *ex situ* blocks/remains for which the exact position in the site is not known and that have been scanned, I have considered the direction of the remains relative to each other. This was conducted on the computer using Avizo 6.3, the software allowing the exploration of the interior of the blocks. If a general orientation is noticed, one cannot tell the geographical direction (north, south, east, and west) but it still provides information about general orientation of the remains. This was used for the MH1 "clavicle block" that was found *ex situ* and for which a 3D rendering was produced.

Estimation of the movement and distances between the bones

In order to estimate the movement that has affected the hominin remains, 3D distances between the *in situ* hominin remains were calculated. This allows an evaluation of the bone dispersion intensity for the MH1 and MH2 individuals.

The 3D distance between two points i and j that both have X, Y and Z coordinates is calculated as follows:

$$\text{Distance between i and j} = \sqrt{[(X_i-X_j)^2 + (Y_i-Y_j)^2 + (Z_i-Z_j)^2]}$$

### *2.4.5. Refitting hypotheses*

Distinction between direct and indirect evidence

During the refitting process of the *ex situ* hominin remains, I used different types of evidence, separated into two categories: direct and indirect evidence. A given hypothesis for the refitting of a specimen based on single direct evidence only has a degree of probability of 100% (or 1). On the other hand, one or even a combination of indirect evidence cannot give a degree of probability of 100% for any proposed hypothesis. Obviously, the combination of a maximum number of indirect evidence increases the degree of probability for one given hypothesis but never to 100%. Some direct evidence can justify both the position *and* orientation of one or several specimen(s) within the deposit, while there is direct evidence for only the orientation. Indirect evidence can elucidate either or both the orientation and position of the bones. Future excavations and expected recovery of missing remains of MH1 and MH2 from *in situ* deposits will permit to test these hypotheses.

Direct evidence for the position and the orientation

One case only allows a degree of probability of 100% for a refitting hypothesis: when the refitting is based on a direct link between an *in situ* specimen and an *ex situ* one. The two elements must match perfectly (no sediment between the bones). This occurs when a bone was broken recently by a mining blown, which has detached a part of the bone and left the remaining part in the deposit.

Direct evidence for the orientation only

Evidence based on sediment contained in a block or a specimen itself, and indicating a flow direction and/or a peculiar organisation of the sediments, can be used to document the original orientation of a block/specimen within the deposit. The sediment contained in the block and/or the specimen can indeed be correlated with the sediment

from the deposit. This provides information for the orientation of the remains but not its exact position (X, Y, Z coordinates) within the deposit.

Indirect evidence for the position and/or orientation

Indirect evidence is based on observations of movement, position and orientation of *in situ* remains on one hand, and of bones present in *ex situ* blocks on the other. This is based on the extrapolation principle: for instance, if the same observation is made for all the *in situ* remains (e.g. low displacement rate of the fossils within the deposit compared to their anatomical position), this observation is equally applied to the *ex situ* remains that have to be refitted. When only indirect evidence is used, the degree of probability of the retained hypothesis can be increased by combining several lines of evidence.

*Movement/transport rate*

The general movement and transport rate for both MH1 and MH2 is low. It is assumed that this is the case for the *ex situ* remains too. Elements anatomically close to each other in the skeleton have been recovered in close proximity (this is true for both MH1 and MH2; see the results in Chapter 7). This includes small elements easily movable (e.g. elements from the "clavicle block" for MH1 or first ribs for MH2).

*Disarticulation order and anatomical logic*

MH2 shows a low level of disarticulation (some joints are still preserved, including fragile joints, such as the right hand and knee). This seems to indicate that the whole skeleton was buried before an advanced state of disarticulation. Therefore, the criteria of low degree of disarticulation is also applied as a proxy for refitting the *ex situ* MH2 bones. In other words, the low degree of disarticulation is used as an argument to place the *ex situ* bones close to their normal anatomical position.

*General orientation and position of the bones*

The position of the whole body suggested by *in situ* bones is used as a proxy to refit *ex situ* bones. This argument is applied in combination with the two previous ones (low transport rate and negligible disarticulation and dispersion). For instance, the position of the bones inside the "arm block" indicates that the upper part of MH2 was facing south and positioned slightly obliquely to the horizontal, while the position of the femur inside the block is consistent with the right leg flexed with the knee pointing east.

Figures illustrating all the hypotheses for the refitting of the different *ex situ* hominin remains are compiled in Appendix 7. The process followed is an application of all these criteria. I proceed first with MH1 remains and then with MH2 remains.

### *2.4.6. Creation of a 3D hypothetical model for refitting the hominin remains in the deposit*

The creation of a 3D model of the cave, including 3D renderings of the hominin remains in their original *in situ* burial position, is based on a probabilistic and hypothetical approach. The final 3D model represents what is considered to be the most likely scenario, for which several lines of evidence exist. The process followed is divided into several steps.

Firstly, 3D renderings (saved as .stl files) of all the hominin remains were created using Avizo 6.3 software. Secondly, using these 3D renderings and based on the digital record of the preparation process, 3D models of the different blocks were produced. Hence, 3D models of the "arm block" (MH2), the "skull block" (MH1), the "ilium block" (MH1) and the "clavicle block" (MH1) were created. In order to do so, all the 3D renderings of the bones found together in the same block were opened in Avizo 6.3 and then positioned one by one according to their original position within the block from which they were recovered. Once all positioned, the files were merged together in order to create a single .stl file that contains all the bones and can be exported. Thirdly, the *in situ* hominin remains for which the exact coordinates are known (MH2 "arm block" and fibula shaft,

MH1 vault fragments, incisor and metatarsals) were placed in a 3D grid. The "arm block" was used as a reference point. The other *in situ* remains were automatically positioned by the software, by entering the coordinates. Then, all *ex situ* remains or groups of remains (i.e. MH1 "skull block" and "clavicle block") were positioned relative to the *in situ* ones. All the different possible positions for each block were successively considered and the most likely retained. To decide, in each case, which position was the most appropriate, I based my decision on field information, geological and geomorphological evidence, as well as the digital record of the general orientation and position of bones found *in situ* and bones found in blocks. Finally, when the 3D model was completed, with each bone and group of bones in their most likely position, all the files were merged into one single .stl file. A 3D rendering (.obj file) of the site (Pit 1) was produced using Photoscan software, which can produce a 3D rendering of any object using only 2D pictures. The two files (i.e. hominin remains and deposit) were opened together and combined to produce the final 3D model.

## 3. FORENSIC SCIENCES

### 3.1. Definition

The adjective forensic (from Latin *forensis*, meaning "in open court, public") relates to or denotes "the application of scientific methods and techniques to the investigation of crime" (Oxford English Dictionary). In other words, all forensic disciplines - and they are legion – contribute to the understanding and interpretation of the events surrounding a crime and of the causes and conditions of death of the victim. The results of a forensic investigation help with the identification of the person(s) and/or factors responsible for the death of the victim, in order to provide evidence in the context of a court case.

Forensic sciences, or "forensics", are subdivided into numerous disciplines, including forensic botany, forensic seismology, forensic geology, forensic astronomy, forensic chemistry, forensic accounting, forensic entomology, only to mention a few. The following sections provide a brief description of the sub-categories of forensic sciences of interest to the present research, namely forensic anthropology, forensic archaeology and forensic

taphonomy, together with their field of applications and their methodology. This constitutes the contextual background in which the new concept of *palaeoforensic taphonomy* will be introduced at the end of this chapter.

## 3.2. Forensic anthropology

### *3.2.1. Creation of the discipline and definition*

Forensic anthropology is a subsection of forensic sciences that applies methods and techniques of physical anthropology and human osteology in the investigation of criminal cases. It was officially recognised as a new section of forensics in 1971, during a meeting of the American Academy of Forensic Sciences, under the influence of Ellis Kerley, Clyde Snow and William Bass, who created the Physical Anthropology section of that Academy (Snow, 1982; Ubelaker and Hunt, 1995; Beary and Lyman, 2012). The field of forensic anthropology has since undergone many developments and is now a well established and recognised discipline (e.g. Ubelaker and Hunt, 1995; Beary and Lyman, 2012).

### *3.2.2. Applications and objectives*

In some legal cases, the bodies are so badly preserved (e.g. mutilated or burnt) or in such an advanced state of decay that the help of a specialist in human anatomy and osteology is required. Physical anthropologists working on a forensic case will address the following questions: identification of the remains (are they humans, and how many individuals are present); description of the physical characteristics of the victim(s), which can serve in their identification (estimation of the sex, age, race, stature, and body weight); detection of anatomical anomalies, such as pathologies, signs of disease or injury, which can also contribute to the identification of the victim; evaluation of the time of death; and determination of the causes (e.g. strangulation, gunshot, drowning) and manner (natural, homicide, suicide, accident, unknown) of death (Snow, 1982).

## 3.3. Forensic archaeology

### *3.3.1. Creation of the discipline and definition*

Forensic archaeology is the application of archaeological methods and techniques to the investigation of criminal and death cases (Morse *et al*., 1976). It was recognised as a subsection of forensics, and specifically of forensic anthrolopology during the seventies and has since undergone significant developments (e.g. Dupras *et al*., 2011).

### *3.3.2. Applications and objectives*

The application of archaeological methods is required in the case of buried individuals. Archaeological skills, in terms of excavations and collection of human remains and all available contextual information, can prove very useful in understanding the context of a crime/burial scene (Morse *et al*., 1976; Dupras *et al*., 2011). The role of forensic archaeologists is to locate possible areas where the victims might have been buried, to interpret the context of the crime scene, and to understand the role played by postdepositional processes with regard to the crime scene transformation. This includes a detailed description of the crime scene, using methods traditionally used in archaeology, such as mapping and drawing of sections and plans, in order to show the exact position of the human remains and associated objects. It also includes careful excavation of the remains, using classical archaeological techniques, characterised by a great degree of precision. Thus, all human remains and evidence (any elements and objects associated with the human remains) are collected, and all relevant information destroyed by the excavations are recorded (e.g. nature of the soil and stratigraphy of the burial context, orientation and exact position of the remains) (Dupras *et al*., 2011).

## 3.4. Forensic taphonomy

### *3.4.1. Creation of the discipline and definition*

Forensic taphonomy is the application of taphonomic methods and techniques to the investigation of a criminal case. It has developed dramatically in the past two decades, as attested by the increased number of publications (e.g. Dirkmaat *et al*., 2008; Beary and Lyman, 2012). Taphonomy plays an important role in forensic cases as it permits investigators to distinguish postmortem modifications that are a consequence of natural processes, unconnected to the crime, from those that are a crucial part of it (Ubelaker, 1997; Dirkmaat *et al*., 2008; Beary and Lyman, 2012).

### *3.4.2. Applications and objectives*

As a forensic discipline, forensic taphonomy determines the identity of the victim and to understand the proceedings of a crime. In a recently published paper, Beary and Lyman (2012) review five goals of the forensic taphonomists, which are to (1) determine whether or not the remains recovered belong to a crime case and are therefore of forensic significance; (2) estimate the postmortem interval (PMI), which is the time between death and recovery; (3) explain how the remains arrived at the place where they were discovered; (4) identify which actions have been conducted to hide the identity of the victim or of the whole crime; and (5) determine which taphonomic factors have had an impact on the remains and how they can "affect (positively or negatively) the investigator's ability to glean information about the victim or the crime" (Beary and Lyman, 2012). Most of the studies in forensic taphonomy available in the literature have addressed questions relating to decomposition of cadavers (e.g. rate, modalities, effects, estimation of PMI, and influence of environmental factors) (e.g. Haglund and Sorg, 2002; Beary and Lyman, 2012).

# 4. DEFINITION OF A NEW CONCEPT: PALAEOFORENSIC TAPHONOMY

## 4.1. Definition and objectives

### *4.1.1. General definition*

Here, I propose and define a new field of research, which finds its inspiration in the previously described disciplines, namely vertebrate taphonomy and forensic anthropology, archaeology and taphonomy. This new exploratory field of research, which I do not yet consider as a new discipline, since it only applies to the case of two hominin skeletons, is investigated in this research project, and will undoubtedly be further developed in the future, as new discoveries of well preserved hominin fossils take place. I name this concept "palaeoforensic taphonomy". As a research area, its aim is to follow a forensic approach to conduct taphonomic investigations on fossil skeletons that are well preserved and complete enough to reconstruct their burial posture. Using taphonomic methods, it seeks to understand the conditions, timing and processes of burial for fossil vertebrate remains that were recovered in a palaeontological context, where each individual skeleton is considered as a unique case. The ultimate goal, as in a forensic case, is to understand the cause and context surrounding the death and burial of the individual skeleton.

### *4.1.2. Differences with traditional vertebrate taphonomy and with biostratinomy*

I refer to this new concept as "taphonomy" because it uses methods and techniques traditionally used in vertebrate taphonomy, namely palaeontological, physical and spatial studies of the fossils. I also refer to it as taphonomy because it aims at understanding some of the processes that are involved in the transformation of organisms from the biosphere to the lithosphere. Vertebrate taphonomy is the study of the changes affecting one or several organism(s) from the moment of death to the time of recovery and curation; it serves to identify which elements have been lost and which have been modified between these two stages (e.g. Efremov, 1940; Lyman, 1994; Beary and Lyman,

2012). Palaeoforensic taphonomy differs from traditional vertebrate taphonomy because it focuses mainly on events surrounding the period between death and burial and during burial, rather than between burial and recovery. Vertebrate taphonomy has "little need to consider the immediate postmortem changes to a deceased organism due in part to the long temporal span separating the investigator from the specimen under study" (Beary and Lyman, 2012); rather, vertebrate taphonomists focus more on understanding the events and changes taking place *after* burial (Lyman, 1994; Beary and Lyman, 2012). With palaeoforensic taphonomy, attention is given primarily to perimortem and immediate postmortem processes, which have affected an individual recovered in a fossil assemblage.

Biostratinomy, a concept first defined by Weigelt (1927), presents similarities with palaeoforensic taphonomy. It is also a sub-discipline of taphonomy, which focuses on the processes that affect animal remains between the moment of death and the moment of burial (e.g. Behrensmeyer *et al*., 1992; Fernández-López and Fernández-Jalvo, 2002). However, the main goals of biostratinomy concern palaeoecological, palaeobiogeographical and evolutionary questions, which is not the case of palaeoforensic taphonomy (see below 4.1.5. Objectives and implications). Palaeoforensic taphonomy is primarily interested in reconstructing and understanding the moment of the burial itself and uses contextual information about the deposit from which the fossils were recovered, such as sedimentological, geological and palaeontological data (e.g. about the associated faunal material) to achieve this goal, while biostratinomy tends to consider information about the processes that have modified the fossils, from the death of the animal to its burial, in order to reconstruct the physical context (i.e. type of environment, climatic conditions, geology of the locus of burial) in which they took place (see for instance Behrensmeyer *et al*., 1992).

### *4.1.3. Why "palaeo-forensic"?*

I refer to this new field of research as "forensic" because the main goal is to understand the conditions and context of the burial and ultimately the causes of death; in other words to determine the biotic and abiotic agents and factors that led to the death and the burial of the individuals. As in a forensic case, the identification of the "victim" and the reconstruction of the "crime" and the "crime scene" are the crucial points of the investigation. Obviously, in the context of fossil hominins that died almost 2 million years ago, the notions of a legal case, court and trial have no significance. This explains the addition of the prefix "palaeo-", which means ancient, and implies that it only applies to cases from the fossil record and therefore loses any judicial meaning.

### *4.1.4. In which case can it be applied?*

The concept of palaeoforensic taphonomy is developed as an answer to tackle the very specific case of the well-preserved hominins from Malapa; MH1 and MH2. Its field of application is limited so far to these two individuals. However, more individuals from the Malapa site should be recovered as excavations progress, and some near complete skeletons of non-hominin animals have already been recovered. Other deposits, such as the Silberberg Grotto at Sterkfontein, have provided well preserved hominin remains, namely StW 573, "Little Foot" (Clarke, 1988, 1998, 1999, 2008). It is reasonable to expect that discoveries of new fossil localities containing *in situ* and well preserved hominins will be made in the future. Together with an accurate collection of contextual information and spatial data, a palaeoforensic taphonomic approach could be applied. Some conditions are required in order to maximize the chances of getting informative results when applying this new approach. Three conditions need to be met: (1) the individual has to be represented by a complete or near complete skeleton, (2) it must be recovered *in situ* (or, alternatively its exact provenance inside the deposit must be known), and (3) any spatial

information about the position, orientation, angle and direction of the remains inside the deposit must be recorded.

### *4.1.5. Objectives and implications*

As mentioned previously, the primary goal of palaeoforensic vertebrate taphonomy is to reconstruct the *burial* of a given fossil, which could potentially lead to understanding its *death*. This primary goal is subdivided into various questions that need to be addressed:

- Is the posture in which the fossil was recovered consistent with a *death* posture or with a *burial* posture? This requires determining whether the deposit, from where the fossil comes, is consistent with the location of death or with the location of burial, if the two differ.
- If the fossil is recovered in a secondary deposit (parautochthonous or reworked), which agents have displaced it from the primary deposit? In other words, what kind of transportation occurred between death and burial (e.g. water, scavengers, gravity)?
- If transportation has occurred, what was the degree of decay and disarticulation of the skeleton when it happened?
- What is the rate of burial and how much time went by between death and final burial? This is similar to the estimation of post mortem interval (PMI) in forensic cases.
- What was the degree of decay when the skeleton was completely buried?
- What was the stage of disarticulation when the skeleton was buried?
- What was the context of the burial in terms of environmental conditions (including location, for instance in water, in a cave chamber, in mud; temperature; humidity; level of light)?
- Which factors have affected the skeleton pre- and post burial (e.g. contribution by scavengers, insects, bats, action of water, gravity)? The effect of each agent must be chronologically ordered.

Understanding why and how a fossil was buried provides direct information about the events that preceded the burial. Similar to a time machine going back step by step, it brings us closer to the moment of death. The results of palaeoforensic taphonomic investigations also provide information about the exact state of decay and disarticulation when the body was finally buried. This can help in the evaluation of the possibilities of recovering missing elements and predicting where to look for them. This can also prove useful in predicting where evidence of soft tissues or amino acids may be present.

#### *4.1.6. Methodology*

Palaeoforensic taphonomy follows a forensic approach, which consists of collecting as much evidence as possible. The main aim is the reconstruction and study of the burial posture, in the context of a faunal assemblage, in a specific deposit, at a given fossil site. The three dimensional approach is therefore crucial and seeks to reconstruct the exact position of the bones inside the deposit, in their original place, orientation and angle. The geomorphology of the site and the geology of the deposits must also be considered, as they document the context of the "crime scene". Classical taphonomic methods of inquiry are required, such as description of the associated fauna, in terms of composition, general preservation, estimation of the body part survival patterns (i.e. palaeontological approach), as well as a detailed microscopic analysis of the bone surfaces and study of the breakage patterns (i.e. physical approach).

### 4.2. Death and burial postures of fossil vertebrates

#### *4.2.1. Introduction*

When vertebrate skeletons are preserved well enough to describe their burial position, relevant information regarding the causes and conditions of burial can be discussed. The causes of death, conditions in which a corpse is buried (e.g. on land, in mud, in water, in a confined space or on an open surface), and preservation processes all condition the position of the skeleton at the time of recovery. In the fields of vertebrate

palaeontology, funerary archaeology, and forensic anthropology, the position of a corpse/skeleton is used to document some aspects of death and burial, which in return can prove useful to document past behaviour, ecology, and in the case of humans, cultural traditions or crime scenes.

### *4.2.2. Palaeontological contexts*

Occasionally, the fossil record yields articulated or near-articulated and well preserved vertebrate skeletons, which present a combination of all or some of the following characteristics: very little or no weathering, absence of carnivore damage, presence of complete and/or near complete elements, and bones in anatomical position. These cases are rare and occur only when specific conditions, associated with the modes of burial and preservation of the skeletons, are met. The preservation of articulated specimens in the fossil record is consistent with individuals that were buried rapidly, before complete decomposition of soft tissues (e.g. skin, muscles, tendons, ligaments), which were still holding the bones together (Gradziński, 1969; Schäfer, 1972; Maureille and Sellier, 1996; Gargett, 1999; Duday, 2009). It is also consistent with carcasses that remained undisturbed in their primary deposit until their recovery. In other words, they represent animals that were preserved in their burial and sometimes in their death positions. They have not been subjected to a long period of subaerial exposure; they have not undergone significant water transport, they have not been scattered or significantly chewed on by scavengers, damaged by erosion, wind or sun. Such cases of quick burial followed by little or no perturbation usually happen during catastrophic events such as floods (Smith, 1980, 1987, 1993; Weigelt, 1989; Smith and Evans, 1996; Rogers *et al*., 2007). They can also be associated with climatic changes, such as an increase of arid conditions causing droughts (Shipman, 1975; Rogers, 1990; Smith, 1995; Smith and Ward, 2001; Rogers *et al*., 2007). Animals drowned in waterlogged sand and mud tend to preserve well (e.g. Weigelt, 1989 and Ochev, 1995; Rogers *et al*., 2007). The combination of catastrophic events or rapid climate change with specific animal behaviour, such as living in an underground burrow,

can increase the chances of good preservation, by preventing access to the skeleton by scavengers and other destructive taphonomic agents (Smith, 1987, 1995; Smith and Evans, 1996; Adbala *et al*., 2006; Botha-Brink and Modesto, 2007).

In the following sections I describe burial positions observed among well preserved vertebrate fossil skeletons and frequently mentioned in the palaeontological literature. The analysis of the burial posture serves to interpret causes, conditions and timing of burial, which lead to understanding causes and conditions of death. In some cases, studying the burial position also provides information about the behaviour and ecology of extinct species. An exhaustive review of all cases described in the literature is beyond the scope of this project. Rather, a sample of examples is provided here of the most commonly described types of burial positions, together with their taphonomic interpretations. Six types of fossil postures are regularly mentioned in the literature: "curled-up" (Smith, 1987, 1993, 1995; Smith and Ward, 2001; Damiani *et al*., 2003), straight or reflexed spinal curvature (Smith, 1993), opisthotonic posture (head, neck and spinal column in an arched position) (Faux and Padian, 2007; Reisdorf and Wuttke, 2012), "dorsal up" (Ochev, 1995; Smith and Evans, 1996; Abdala *et al.*, 2006; Botha-Brink and Modesto, 2007), "belly up" (Ochev, 1995; Stanford *et al*., 2011; Fordyce *et al*., 2012) and "head up" positions (Smith, 1980; Fordyce *et al*., 2012). A distinction has to be made between passive and rigid positions (Gradziński, 1969; Dodson, 1973; Weigelt, 1989). The former, namely ventral ("dorsal up") and dorsal ("belly up") positions are passive positions, which are consistent with animals that were buried quickly after death, but after *rigor mortis* set in. In other words, muscles and ligaments were relaxed and the conditions of burial (e.g. in water) lead to the placement of the corpse in an unbent position with the limbs spread. Consequently, passive positions document the conditions of burial rather than the causes of death. On the other hand, a rigid position is consistent with animals that were buried in a constrained position caused by *rigor mortis*, desiccation, drowning or failure of the nervous system (Dodson, 1973; Weigelt, 1989; Faux and Padian, 2007), as in the case of animals found in "curled-up", "head up", or

opisthotonic postures. The animals were buried (e.g. trapped in mud, covered by sediments) while *rigor mortis* was still active (in the case of opisthotonic posture), or while they were still alive and died unexpectedly (e.g. flood or accidental drowning, as can be the case with skeletons showing a "head up" or a "curled-up" posture). The analysis of rigid positions constitutes therefore a direct access to the causes and conditions of death.

The following paragraphs provide more detailed information about each of the most commonly observed postures in the fossil record for articulated vertebrate skeletons.

"Curled-up" posture

The curled-up posture, consistent with taphonomic class "A" described by Smith (1980, 1993), is generally associated with animals that died in their burrows, under various circumstances, especially drowning by flooding (Smith, 1980, 1987, 1993, 1995; Damiani *et al*., 2003). This posture can indicate preservation during aestivation or hibernation (Smith, 1980) and is usually used as an argument to demonstrate burrowing behaviour, especially when the burrows are not preserved (Smith, 1995). Abundant mammal-like reptiles from the Permian, namely dicynodonts, such as *Diictodon* (Smith, 1980, 1987, 1993) and cynodonts, such as *Thrinaxodon* (Smith, 1995; Damiani *et al*., 2003) have been recovered in a curled-up posture. They are found in floodplain deposits, usually associated with channel-bank deposits (Smith, 1980, 1987) and are interpreted as individuals that either died during a catastrophic flood or were dead and already decomposing when the flood happened. When preserved, the skeletons are usually found in the terminal chambers of their burrows (Smith, 1987, 1993; Damiani *et al*., 2003). Since the curled-up posture is consistent with individuals already dead in their burrow or that have drowned during a flood event, it is associated with a burial position and a primary deposit (site of death). There is no transportation, no scattering and the duration of the *post-mortem* pre-burial period is very short (Smith, 1993). Curled-up skeletons of *Lystrosaurus* are found in the Permian-Triassic boundary sedimentary units of the Karoo Basin. The posture of these skeletons is used as an argument to defend the hypothesis of their burrowing habits

(Smith, 1995). It can indicate desiccation and is interpreted as evidence of rapid and drastic climatic changes taking place at the end of the Permian, in the form of drying causing droughts and decrease of vegetation (Smith, 1995; Smith and Ward, 2001).

Straight or reflexed spinal curvature

Complete skeletons recovered with straight or reflexed spinal curvature (taphonomic class "B", in Smith, 1993) are described for some Permian fossil therapsids recovered in the Karoo Basin. They are considered as animals that died in their burrow and mummified; they are associated with a rapid burial and no transportation (Smith, 1993).

Opisthotonic posture

Articulated skeletons of animals with a long neck and tail, such as fossil birds, dinosaurs, pterosaurs and some placental mammals are sometimes recovered in an opisthotonic (from the Greek *opistho*, behind and *tonos*, tightening) posture (e.g. Moodie, 1923; Weigelt, 1989; Faux and Padian, 2007; Reisdorf and Wuttke, 2012), which can be described as an "extreme, dorsally hyper extended posture of the spine, characterised by the skull and neck recurved over the back, and with strong extension of the tail" and is consistent with a stiffening of the vertebral column (Faux and Padian, 2007, p.1). In clinical cases, the opisthotonic posture is explained as the direct result of opisthotonus, which, in the medical literature, refers to both the opisthotonic posture and the symptoms causing them. Causes of death associated with opisthotonus include asphyxiation, lack of nourishment or essential nutrients, environmental toxins or viral infections (see Faux and Padian, 2007), which all afflict the central nervous system, causing the body to contract in an opisthotonic posture. A multitude of hypotheses have been proposed to explain this posture among fossil skeletons, and its exact origin is still debated (see for instance Faux and Padian, 2007; Reisdorf and Wuttke, 2012). Possible explanations include mostly postmortem factors, such as the result of *rigor mortis* (Gillette, 1994; Laws, 1996 in Faux and Padian, 2007), a natural sleeping position in which the animal died (Heinroth, 1923),

the relaxation of the muscles after death (Wellnhofer, 1991 in Faux and Padian, 2007), the consequence of death and dive of animals stuck in mud (Deecke, 1915 in Faux and Padian, 2007), the effect of current flow operating on a carcass that has sunk (de Buisonjé, 1985; Frey and Martill, 1994 in Faux and Padian, 2007), the effect of postmortem subaerial desiccation followed by the contraction of the tendons of the back of the neck (Weigelt, 1989), and hyper saline dehydration of tissues, which causes a contraction of the tendons from the neck (Schäfer, 1972; Seilacher *et al*., 1985; Wellnhofer, 1991: in Faux and Padian, 2007; ). Contrary to these explanations, a recent study by Faux and Padian (2007) proposes that the opisthotonic posture is not the consequence of a postmortem process but the result of a perimortem process, namely death throes, as already suggested by Moodie (1918, 1923 in Faux and Padian, 2007). *Rigor mortis* would preserve the position of an animal that died in opisthotonus and this posture would be maintained in the case of burial quickly after death (Faux and Padian, 2007). Their study is, however, not supported by experimental data. They do not prove that an opisthotonic posture is caused by a perimortem process; the data presented serve only to invalidate previous hypotheses, such as drying of soft tissues or hypersaline dehydration of tissues. Their hypothesis, even though generally accepted (e.g. Eberth *et al*., 2010 in Reisdorf and Wuttke, 2012; Georgi and Krause, 2010; Elgin *et al*., 2011; Lingham-Soliar, 2011), has been challenged by others. For instance, Reisdorf and Wuttke (2012) maintain that opisthotonic posture observed in the fossil record is the result of a postmortem process, occurring in an aquatic environment, and has therefore nothing to do with the cause of death being related to opisthotonus. A recent experiment on plucked chickens demonstrated that immersion in water cause directly lead to opisthotonic posture (Cutler *et al*., 2011).

<u>"Dorsal up" posture</u>

A dorsal up posture is consistent with burial in life position (Ochev, 1995; Smith, 1995; Smith and Evans, 1996; Botha-Brink and Modesto, 2007), whereby the body has been deposited in a vertical manner, with the limbs going straight down on one or two sides

(Ochev, 1995). This posture has been described for abundant pareiasaur skeletons from the Late Permian locality of Kotel'nich in Russia (see Ochev, 1995). Various hypotheses have been proposed to explain the origin of the posture. The animals could have been mired in the mud and, unable to move, died there. They could also, if one accepts aquatic habits for this species, have died inside the lake because of drying up of the water. Alternatively, they could have lived and died inside the lake from natural causes, sunk and eventually became trapped in the mud present at the bottom of the lake (see Ochev, 1995). The hypothesis considered as the more plausible is the existence of muddy plains and animals, especially weak and young individuals, being bogged down, dying there and becoming preserved in a vertical position, back up and legs down. In a different context, dorsal and dorsal-side up positions have been described for taxa of Permian reptiles (Smith and Evans, 1996), cynodonts (Adbala *et al*., 2006) and pelycosaurs (Botha-Brink and Modesto, 2007) are interpreted as evidence of group denning behaviours, as illustrated by the way the skeletons are aggregated (Smith and Evans, 1996; Abdala *et al.*, 2006; Botha-Brink and Modesto, 2007).

"Belly up" posture

Skeletons found in a belly up posture are interpreted as animals that have drowned or died close to water. Once in the water, gasses associated with the decomposition of the abdomen and its content cause the body to float, belly up. The carcass then sinks and gets buried in that position (Ochev, 1995; Stanford *et al*., 2011; Fordyce *et al*., 2012). Belly up positions are associated with catastrophic flood events, either causing animals to drown (Ochev, 1995) or collecting dead animals decomposing on the surface (Fordyce *et al*., 2012). It can also be associated with accidental drowning, as in the case of an immature dinosaur (nodosaurid, *Propanoplosaurus marylandicus*) that was recovered in the form of natural impressions in the sediments of the Lower Cretaceous of Maryland, USA, in a belly up posture (Stanford *et al*., 2011). To explain the burial position, the following scenario has been proposed: the postnatal individual drowned near its nest, in shallow water,

floated for a while with bloated belly up due to the decomposition of the internal contents, producing gasses. The carcass consequently sank after the abdomen burst and came to rest on the bed, in the same posture, belly up (Stanford *et al*., 2011).

"Head up" posture

The head up posture is generally described in association with a belly up posture (Fordyce *et al*., 2012), as it is also considered as evidence for animals that were buried while in water (Smith, 1980). The head up attitude observed among pareiasaurians recovered in the Permian sediments of the Karoo Basin was interpreted by Haughton (1919) and Von Huene (1925) as "evidence of back swamp conditions where the semi-aquatic pareiasaurians were often mired and overwhelmed whilst gasping for air" (in Smith, 1980).

### *4.2.3. In archaeological sites*

The position in which human skeletons are recovered from archaeological contexts can be of two types: the death posture, extremely rare since it requires the burial of the body just after death, before any modification can take place; and the burial posture, consistent with the position in which the body was protected after death, either naturally, or through intentional burial. When bodies are recovered in their death attitude, it is possible to determine causes and conditions of death (e.g. Mastrolorenzo *et al*., 2001, 2010; Luongo *et al*., 2003; Bedford and Tsokos, 2012). When bodies are recovered in their burial attitude, information regarding the nature of burial (natural or intentional) can be gathered. In the case of intentional burial, mortuary behaviours of past populations can be documented (e.g. Harrold, 1980; Pearson, 1999; Knusel *et al*., 1996; Roksandic, 2002; Duday, 2009; Pettitt, 2011).

Burial position

The recovery of complete or near complete human skeletons in archaeological sites provokes questions regarding how they came to be there, whether through natural or anthropogenic causes. The identification of the position of the skeleton can be crucial in deciding whether the individuals were preserved accidentally, or if they reflect intentional burial, associated with funeral rituals. This question is especially true in Middle Palaeolithic contexts, where the existence of mortuary behaviours among Neanderthals is a topic of great interest and debate (e.g. Gargett, 1989a, 1999; Koojmans *et al*., 1989; Langley *et al*., 2008; Pettitt, 2011; Sandgathe *et al*., 2011). Together with other elements (e.g. good state of articulation; evidence for intentional protection of the body, clear difference in the sediments), a certain arrangement of the body is considered as evidence for intentional burial (Binford, 1968; Harrold, 1980; Smirnov, 1989; Villa, 1989; Belfer-Cohen and Hovers, 1992; Kimbel *et al*., 1995). Hence, a strongly flexed position of the body or of some body parts, namely the legs and/or the arms, is interpreted by some authors as clear indication of handling of the corpse and intentional burial (Bouyssonie, 1954 in Smirnov, 1989; Binford, 1968; Harrold, 1980; Villa, 1989; Kimbel *et al*., 1995). Burials are generally, but not exclusively, associated with bodies positioned on their backs or placed on one side, whether fully extended or loosely or tightly flexed; the absence of such arrangement (i.e. haphazard arrangement of the body) can be used to demonstrate natural preservation rather than intentional burial (Sandgathe *et al*., 2011). However, the criterion of a specific arrangement of the body to justify intentional burial has been challenged, notably by Gargett (1989a, 1989b, 1999), who, based on the concept of equifinality, argues that unintentional factors and natural causes can also lead to a specific body arrangement. For instance, individuals who died during their sleep have been found in a flexed position (Gargett, 1999).

In more recent contexts, when there is clear contextual evidence of intentional burial (e.g. skeletons found in a funerary complex such as cemetery, presence of grave goods

and elements of ornament, evidence of a void dug to accommodate the corpse, presence of a coffin), the position of the body documents traditional cultural funeral practices around the treatment of the dead, which is why the need of recording such information during excavations has been stressed by some (Duday *et al*., 1990; Roksandic, 2002; Duday, 2009). For instance, the nature of the deposit (primary or secondary) from which the skeleton is recovered can be assessed based on the position of the body (Maureille and Sellier, 1996; Roksandic, 2002; Duday, 2009). Human skeletons in funerary contexts are recovered in a variety of postures (e.g. lying on the back, on one side, sitting down, orientated in a certain direction, extended or flexed), which represent intentional gestures and specific treatment of the dead by the people who buried them (e.g. Harrold, 1980; Pearson, 1999; Roksandic, 2002; Duday, 2009; Pettitt, 2011). Two examples are given here to illustrate how the analysis of body position in a funeral context can provide information about mortuary behaviours. The first example dates from the Late Preclassic period (ca.100 B.C. to A.D. 100) of Mesoamerica (Fowler, 1984). The structure E-7 at Chalchuapa, El Salvador, is a burial mound that has yielded the remains of at least 33 individuals. These individuals are buried in a homogeneous way; face down, arms semi flexed, and right and left carpals and/or right and left tarsals touching. This specific arrangement of the skeletons suggests that the individuals were bound. Together with other contextual evidence, such as the age pattern and the lack of grave goods, this indicates that the skeletons represent victims of ritual sacrifices (Fowler, 1984). The second example concerns prone position in a burial, which is interpreted – again with the contribution of other contextual data - either as a live burial or as a mark of disrespect for the dead from the community, which buried them (Handler, 1996; Bedford and Tsokos, 2012). For instance, the skeleton of a young woman was recovered in the late 16$^{th}$/early 17$^{th}$ century slave cemetery in Barbados, West Indies, in a prone position (Handler, 1996). The author (Handler, 1996) suggests that it could be an indication that this individual was viewed negatively by the community and was therefore “feared or socially ostracised”. This is

confirmed by the absence of a coffin and of grave goods, and by the fact that she is the only individual buried in a prone position in the whole cemetery (Handler, 1996).

Death position

Death position can be preserved in the archaeological record in the case of a catastrophic event, such as volcanic eruption, the most famous example being the eruption of the Mount Vesuvius in AD 79, in Italy. The eruption, of explosive nature, led to the destruction of the Roman towns of Pompeii and Herculanum, together with most of their inhabitants (Mastrolorenzo *et al*., 2001; Luongo *et al*., 2003). The victims and the buildings were covered by a significant layer of ashes and pyroclastic flows, which preserved them perfectly, to the present. To date, a total of 1150 individuals have been excavated, 1044 of which are complete and identifiable (Luongo *et al*., 2003). The individuals have been preserved in the position in which they died. The analysis of body posture among Pompeii and Herculanum victims has allowed a detailed reconstruction of the last moments of life and conditions of death of the victims of the eruption. Various causes of death have been identified (Mastrolorenzo *et al*., 2001, 2010; Luongo *et al*., 2003): suffocation due to ash; collapse of roofs and walls due to the weight of pumice lapilli, which is material projected by the volcano during the eruption and composed of molten or semi-molten lava; trapped by pyroclastic density currents (PDCs), which are "turbulent hot mixtures of fine ash and gas flowing down volcano slopes at high speeds" (Mastrolorenzo *et al*., 2010); and thermally induced shock due to the heat of the PDCs. To each type of death corresponds a certain position of the body, consistent with self protection, agony contortions, or natural postures ("life-like" and "sleep-like" stances) (Mastrolorenzo *et al*., 2001, 2010; Luongo *et al*., 2003). Some bodies have been recovered supporting their head and sometimes their chest with their arms, in an attempt to keep their head above the pyroclastic flow (Luongo *et al*., 2003). Others bodies display a characteristic hyper flexion, or *flexor reflex*, of the hands and feet interpreted as a consequence of a thermally induced contraction of the muscles. This is explained by the

very sudden death caused by the surge of pyroclastic flow, instantaneously followed by the contraction of muscles and tendons. An ash fall occurring just after and causing a sudden drop in temperature fixed the bodies in that position (Mastrolorenzo *et al*., 2001). Some bodies show an extreme state of contraction, or "pugilistic attitude", with the limbs flexed and the spine extended (Mastrolorenzo *et al*., 2001), which is characteristic of people exposed to very high heat (minimum 200-250°C) leading to an instantaneous death, such as fire victims and deaths in pyroclastic flows (Baxter, 1990; Knüsel *et al*., 1996).

### 4.3. The early hominin fossil record and Malapa

The scarcity of well-preserved, complete or near complete, articulated skeletons in the early hominin fossil record, together with other factors, such as a lack of information concerning the provenience of the fossils (e.g. in the case of early excavations, or when the material is recovered *ex situ*), has led to an absence of information regarding the posture of the skeletons. Hence, until now, it has been impossible to accurately reconstruct causes of death, and conditions and timing of burial for early hominins. The Malapa hominins are well preserved and comprise complete and near complete bones, sometimes still in articulation. Some remains were recovered *in situ*, and there are enough sources of information to reconstruct their burial posture inside the deposit (see Chapter 7). Together with a detailed microscopic analysis of the bone surfaces, gathering of contextual information, namely geomorphological, geological and stratigraphic, as well as observations on the associated faunal material, it is possible to document the context of the burial, its timing and modalities, and to propose hypotheses concerning the cause(s) and conditions of their deaths.

# Chapter 5. Contextual information about the site and the fauna.

This chapter introduces the context in which the hominins were recovered. It presents the general environment of the site (geographical location, geology and ecology of the area) and close-up description of the cave (geomorphology of the cave, stratigraphy and dating of the deposits), followed by a taphonomic analysis of the non-hominin faunal material that has been recovered and prepared to date (composition of the faunal spectrum and presentation of the general degree of preservation).

## 1. GENERAL SETTING OF THE MALAPA SITE

### 1.1. Geographical location

The site of Malapa is located on the Malapa Nature Reserve in the Cradle of Humankind World Heritage Site (Gauteng Province, north of Johannesburg, South Africa). Geographically, it belongs to the Cradle of Humankind and is located approximately 15 km NNE of the Sterkfontein Caves, on the side of a low hill. Figures 5.1 and 5.2 illustrate the fossil deposits from the Malapa site.

**Figure 5.1.** The Malapa fossil deposits (north view).

**Figure 5.2**. The Malapa fossil deposits (view from the west).

## 1.2. Discovery of the site

The site of Malapa was identified during the course of a geospatial survey in the Cradle of Humankind. This survey was conducted by Lee R. Berger and aimed at locating new fossil-bearing cave deposits in the dolomitic region of the Cradle of Humankind. This involved surveying using satellite Google Earth imagery, and classical pedestrian prospecting. As with other sites in the Cradle, the site of Malapa has undergone some minor mining work at or before the beginning of the 20$^{th}$ century (Dirks *et al*., 2010; Berger, 2012), at a time when the limestone present in these caves was sought after by the gold mining industry, as well as for fertilizer and manufacturing toothpaste (Brain, 1981; Pickering, 2004). Matthew Berger, Lee Berger's son, found the first hominin bone (UW88-1, a juvenile clavicle) on the 8$^{th}$ of August 2008, in one of the blocks of calcified clastic sediment removed by the miners and left at the site. Subsequent to this discovery, miners debris and blocks were collected and prepared, leading to the discovery of more hominins (*Australopithecus sediba*) and associated faunal remains (Berger, 2012).

## 1.3. Geology of the area

Together with other sites in the Cradle of Humankind, Malapa cave is located in the Malmani Subgroup, a stromatolite-rich dolomite formation that formed between 2.64 to 2.50 billion years ago (Martin *et al*., 1998; Eriksson *et al*., 2006 in Dirks *et al*., 2010). The Malmani Subgroup is subdivided into five formations (Oaktree, Monte Christo, Lyttelton, Eccles and Frisco Formations; Eriksson and Truswell, 1974; Eriksson *et al*., 2006). While the majority of the caves in the area are located in the Monte Christo Formation (Partridge, 2000; Herries, 2003), with the exception of Gondolin and Luleche, which occur in the Eccles Formation (Adams, 2006; Adams *et al*., 2007b), the Malapa cave is situated stratigraphically higher, at the top of the Lyttelton Formation (Dirks et al., 2010; Dirks and Berger, 2012). It occurs to the north of a fault line that trends north-south, at the intersection of a north-northeast and a north-northwest fracture (Dirks *et al*., 2010). The floor of the old cave system to which Malapa cave belongs is estimated to have been at least 50 metres below the land surface around 2 My ago (Dirks and Berger, 2012). This cave system has, however, undergone severe erosion since then that has led to the current state, in which only the lower portions of the cave are preserved. Malapa cave is now less than 5 metres deep (Dirks *et al*., 2010).

## 1.4. Ecology of the area

Today, the Malapa site belongs to the grassland biome (Carleton Dolomite Grassland; Figure 5.3), close to the transition to the savannah biome, and is characterised by an abundance of Poaceae and shrubs (Bamford *et al*., 2010). Precipitation, occurring mostly during the summer months, is about 600 mm per year (Mucina and Rutherford, 2006).

**Figure 5.3**. Surrounding landscape (north of the site).

## 2. PRESENTATION OF THE SITE

### 2.1. Geomorphology

The site consists of two localities. The main part (Pit 1) is a cavity 3.3 to 4.4 metres in diametre and about 4 metres deep (Dirks *et al*., 2010), with no roof and a generally square-shape. This is where most of the hominin specimens recovered to date come from. On the east of Pit 1 is another area that has also yielded a few fossil hominins and other animals. This eastern part (Pit 2) is less than 1 metre deep and covers a surface area of about 3 x 5 metres. Pit 2 has also been blasted by the miners, but to a much lesser extent than the main opening, since it is on the surface and very shallow. Pit 1 and Pit 2 are separated from one another by only four metres and consequently share the same geological features. They are considered to be part of the same cave system and to have the same age (Pickering *et al*., 2011).

### 2.2. Geology

Five geological facies, named Facies A to E (from the bottom to the top of the deposit), were identified in the main opening (Pit 1) and described soon after the discovery of the site (Dirks *et al*., 2010). A more recent study provides a geological description of the eastern part (Pit 2) and includes the description of a sixth facies, Facies F (Figures 5.4-5.6; Pickering *et al*., 2011). The six facies are all composed of brownish

calcified clastic sediment or so-called “breccia”, in which fossils are embedded. A flowstone (Flowstone 1) separates the older Facies A and B from the younger Facies C, D and E. A second flowstone (Flowstone 2) has been observed in Pit 2, and is considered to have been deposited after the fossil-bearing sediments of Facies D and E (Pickering *et al*., 2011). Facies F is the youngest; it has been identified in both pits and occurs above Facies E in Pit 1 and above Flowstone 2 in Pit 2.

Some elements of cave walls separate Pit 1 from Pit 2 and consist of two blocks (Figures 5.4-5.6), one of dolomite (block 1) and a second of dolomite and cave sediment (block 2). The composition of the sediments found in block 2 (peloidal grainstone with abundant calcite fenestrae) indicates that it comes from an upper chamber in the cave system that collapsed into the chamber where the hominins were found (Pickering *et al*., 2011).

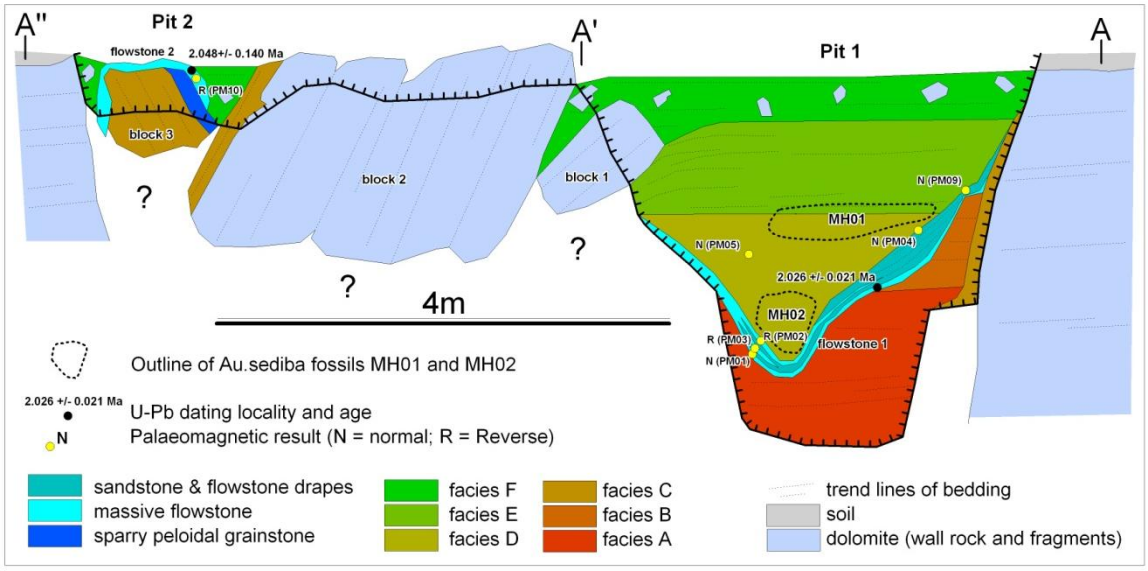



**Figure 5.4**. NE-SW cross-section of the site showing the different sedimentary facies together with the two flowstones (from Pickering *et al*., 2011).

Facies A is present at the bottom of Pit 1 and is the oldest level (Figures 5.5 and 5.6). It consists of dark-brown, moderately sorted, coarse-grained breccia. It is filled with blocks of sparite in which abundant rounded grains (0.5 to 6 mm) of different minerals (chert, quartz, dolomite, iron oxide-coated grains, feldspar and mica schist) are found. The

matrix also contains some ooids, bone fragments and peloids. Bedding is defined by normal and inverse grading. A slightly preferred orientation of rock and bone fragments is observed.

Facies B is mostly preserved on the south and southwestern parts of Pit 1, above Facies A. It consists of grainstone alternating with clastic sandstone. The grainstone contains small rounded peloids (0.4 to 1 mm) composed of fine-grained (0.02 to 0.10 mm) angular quartz grains in a micaceous mud and sparite matrix, as well as a few bone fragments and small pebbles (mostly quartz). Fenestrae lined with sparry calcite are common along horizontal bedding planes. The sandstone grains are rounded and coated with iron oxide. Normal size grading can be observed among the bone fragments in this unit. Finally, there are some small stalagmitic structures that have grown on the grainstone as substrate. A few isolated limestone blocks (<40 cm) are also incorporated in the facies.

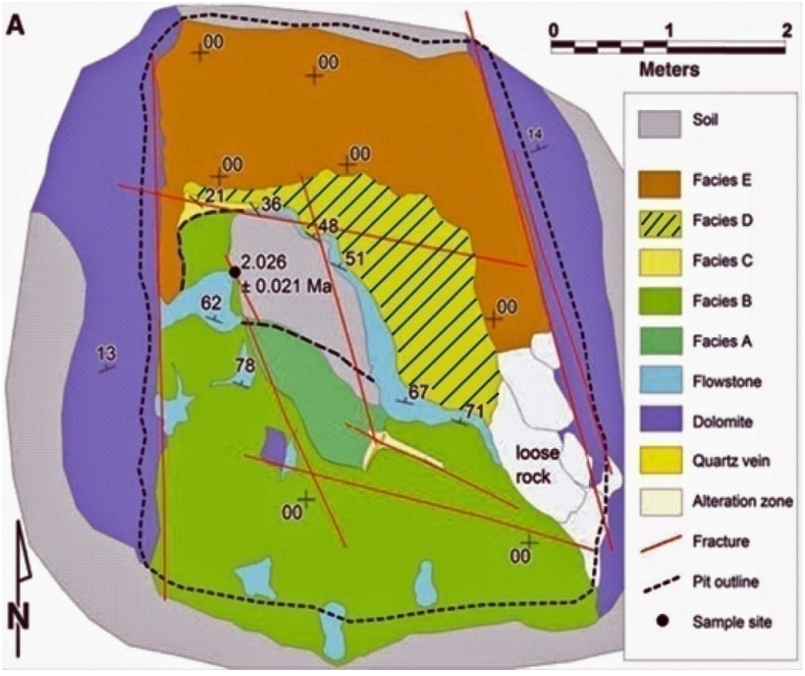



**Figure 5.5**. Five facies identified within the deposit in Pit 1 (from Dirks *et al*., 2010, modified). Most hominin remains come from Facies D (in yellow with green cross-lines on the figure).

Facies C is preserved in the southwest of Pit 1, in the form of a 5-30 cm thick layer above Facies B. This facies is similar to Facies B and occurs after a stage of erosion of Facies A and B, and after the deposition of Flowstone 1. It is characterised by grainstone mainly composed of angular peloids, and contains sub-rounded fragments of quartz, limestone and shale, many of which are iron oxide-coated, as well as bone fragments.

Facies D is on the southern side of Pit 1, extending from east to west (Figures 5.5 and 5.6). On the east side and in the middle, it is located on top of Flowstone 1, whereas on the west side, it occurs directly above Facies C (Figures 3.5 and 3.6). Facies D is a thick (~1.5 metre) and light-brown layer of poorly sorted coarse-grained sandstone cemented by blocky sparite. The framework grains are mostly 0.5 to 2.5 mm in size and consist of quartz, chert, dolomite, peloids and, to a lesser degree, iron oxide-coated grains, ooids, shale and feldspar. There are also some limestone blocks and flowstone fragments. It is the richest facies in term of fossils and contains in particular the remains of the two most complete australopithecine individuals (MH1 and MH2), together with bovids, articulated equid remains and a few carnivore remains.

Facies E occurs on the top of Facies D, in the northern part of Pit 1, from west to east. The majority of the carnivore remains were recovered in Facies E. It consists of calcareous sandstone, similar to Facies D, but with a darker brown colour, finer grained texture, and with a higher degree of sorting displaying horizontal bedding 4 to 15 cm thick. The bottom of Facies E consists of well-sorted, coarse-grained sandstone dominated by 0.6 to 1.5 mm large iron oxide-coated chert, quartz grains and aggregates of peloids. The layer preserves northwest dipping laminations, indicating directional water flow (Dirks *et al*., 2010) and horizontal bedding defined by grain-size variations (coarsening downward), mud stone partings, thin (<1 mm) flowstone drapes and imbricated bone fragments.

Facies F is at the top of the deposit and overlies Facies E in both Pit 1 and Pit 2. It consists of a massive grainstone composed mainly of small peloids. It is horizontally layered and shows graded bedding.

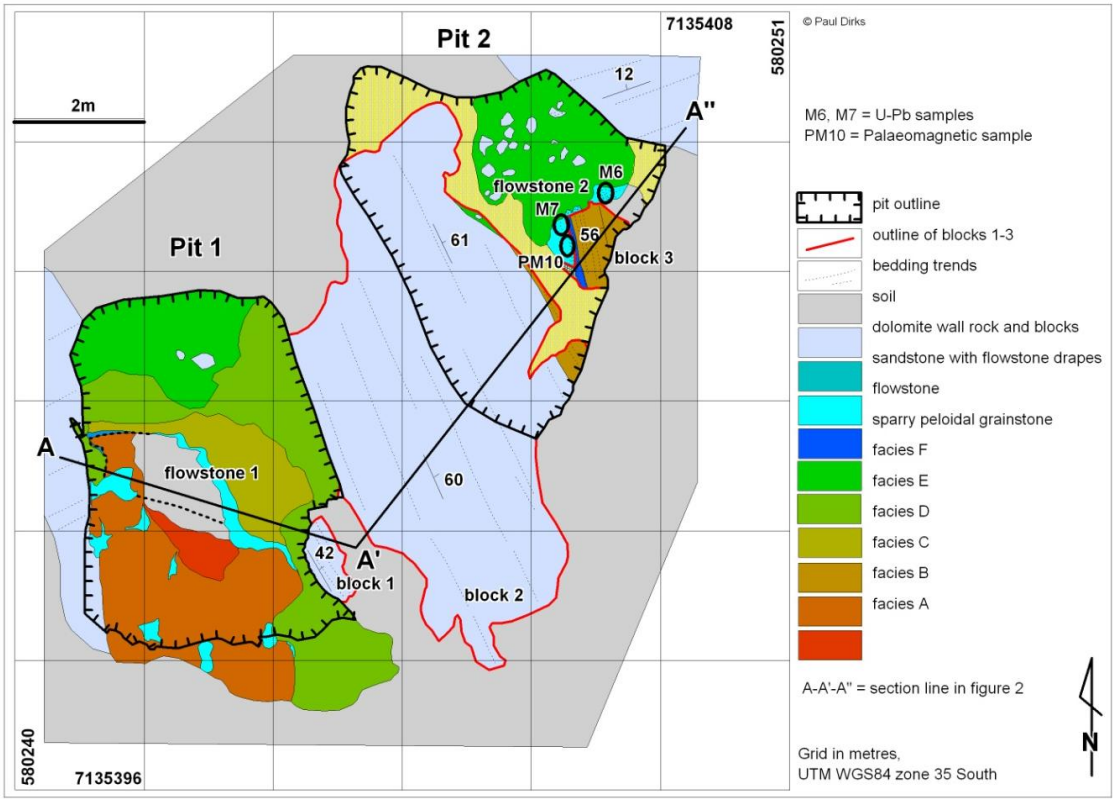



**Figure 5.6**. Geological facies and organisation of the deposit in both Pits 1 and 2 (from Pickering *et al*., 2011).

## 2.3. Formation of the cave and sedimentary deposits

### *2.3.1. Opening of the cave and bone accumulation*

The six-stage cave formation process defined by Brain (1958; 1981; see Chapter 2) may be applied to the Malapa cave system. The main cavity at Malapa (Pit 1) was probably already open to the surface by the time the first sediments (Facies A) were deposited, as indicated by the occurrence of bone fragments as well as peloids interpreted as possible faecal remains (Dirks *et al*., 2010) possibly produced by bats (Paul Dirks, pers. comm.). This was followed by the accumulation of another level of sediment (Facies B). A phase of erosion then affected the deposit, and a flowstone (flowstone 1) formed on top of it, followed by a new stage of sedimentation that led to the formation of three consecutive levels, Facies C, D and E. Another flowstone (flowstone 2) formed and capped the deposit.

A final accumulation of sediment (Facies F) occurred before the cave underwent a severe phase of erosion.

The Malapa cave system was opened along fractures that served as natural traps (Dirks *et al*., 2010; Dirks and Berger, 2012). They would have constituted death traps into which animals, possibly attracted by water present in the cave, would have fallen and died. It is proposed that the hominins fell into an upper chamber and were subsequently carried deeper into the cave by a debris flow, perhaps caused by a storm (Dirks *et al*., 2010). There is geological evidence of a strong water inflow preserved in the sediments of Facies D, such as the presence of isopachous sparite cement, which is an indicator of cementation soon after deposition in a phreatic environment (Blatt *et al*., 2006, in Dirks *et al*., 2010), and the occurrence of allochthonous material mixed with autochthonous cave-derived sediment. The state of articulation and preservation of the hominins is consistent with little transport and rapid burial that took place soon after death. A preliminary observation of the faunal remains shows the absence of carnivore damage and suggests that predators did not access the cave (Dirks *et al*., 2010).

### *2.3.2. Geological evidence for a debris flow*

Several characteristics of the fossil-bearing geological Facies D, E and F have been interpreted as evidence for the action of a debris flow, as well as the deposition of sediments in an aqueous environment (Dirks *et al*., 2010). Facies D and E are composed of water-laid sediments made of sandstone, and contain abundant peloids, which show evidence of mechanical reworking in a water-logged context. Facies E, which overlies Facies D, the geological unit containing the well-preserved hominin remains (MH1 and MH2 specimens), shows a fining upward and preserves northwest dipping laminations indicative of directional water flow (Dirks *et al*., 2010). The presence of isopachous sparite in these two facies is indicative of rapid cementation taking place soon after the deposition of the sediments, in a phreatic environment. Facies D contains allochtonous material, mixed with autochtonous cave sediment, suggesting that this unit deposited

through the action of a debris flow carrying elements from outside the cave and mixing them with elements from inside (Dirks *et al*., 2010). Facies E, on the other hand, is mostly composed of autochtonous sediment. This implies that after the debris flow occurred, the cave filled horizontally with sediments. Facies F, which is a grainstone deposit, also shows horizontal layering and graded bedding (Pickering *et al*., 2011).

### 2.4. Dating methods and age of the deposits

Three dating methods (biochronology, U-Pb and palaeomagnetism) were used and have produced an age of 1.98-1.75 million years for Facies D, the unit containing most of the hominin remains (Dirks *et al*., 2010). The occurrence of extant faunal species that only occur in Africa from 2.36 Ma (i.e. *Felis silvestris*, *Parahyaena brunnea*, *Lycaon* sp., *Tragelaphus* cf. *Strepsiceros* and *Equus* sp.) and of the extinct sabre tooth cat *Megantereon whitei*, which disappeared at 1.5 Ma, provided a first age bracket between 2.36 and 1.5 Ma years for Facies D (Dirks *et al*., 2010).

Flowstone 1, which underlies Facies D, E and F, was sampled and dated using U-Pb methods. This provided an age between 2.024 and 2.026 Ma.

Finally, several samples of the deposit, from below, inside and above Facies D, were analysed for palaeomagnetism. Flowstone 1 preserves a reverse polarity while Facies D shows on its base a normal polarity followed by an intermediate polarity. The normal polarity is interpreted as the beginning of the Olduvai Subchron, dated at 1.98-1.75 Ma (Dirks *et al*., 2010).

Subsequent analyses (U-Pb and palaeomagnetism) of Flowstone 2, capping the deposit with the exception of Facies F, allowed a refinement of the age of the fossil-bearing sediments in Facies D and E (Pickering *et al*., 2011). The U-Pb technique provides an age of 2.048 +/- 0.140 Ma (age rank between 2.19 and 1.91 Ma). The palaeomagnetism reveals that Flowstone 2 has a reverse polarity, which, together with the U-Pb dates, indicates that it formed before the beginning of the Olduvai normal polarity subchron at 1.95 Ma.

Flowstone 1 was dated at 2.026 +/- 0.021 Ma and shows a reverse polarity. Consequently, the hypothesis proposed (Pickering *et al.*, 2011) to explain the normal polarity of Facies D and E is that they were deposited during the Pre-Olduvai excursion, at 1.977 Ma (Pickering *et al*., 2011). The duration of the Pre-Olduvai event has been estimated at 3000 years (Channell *et al*., 2002), which provides an age range for the deposit of the fossil-bearing sediments at 1.977 +/-0.003 Ma.

## 3. NON-HOMININ FAUNAL MATERIAL: GENERAL PRESERVATION

The faunal assemblage studied here is mainly composed of fossils that come from *ex situ* blocks of calcified sediment. Their attribution to a particular fossil-bearing stratigraphic unit has not yet been established. As mentioned earlier (see Chapter 4), the priority was given, during excavation and block preparation, to the collection of hominin/primate remains. It is therefore premature to publish a detailed taphonomic study of the faunal assemblage, as it currently represents a small and biased percentage of the complete faunal assemblage, which will be revealed by future excavations. It is also likely that the taphonomy of the faunal material will vary from one facies to the next, which might be of different age, and possibly characterised by different modes of accumulation. Future excavations will increase the size of the faunal assemblage and provide *in situ* material that will be studied in order to provide a comprehensive and complete taphonomic analysis of the whole faunal assemblage. This is not the aim of the following section. Here, the objective is to describe the general state of preservation of the available faunal material in order to determine whether or not other non-hominin individuals record a similar state of preservation as MH1 and MH2. In other words, if there is an occurrence in the faunal material of complete and near complete bones, articulated specimens, antimeric sets of bones, and fossils showing a well-preserved bone surface. This section serves to provide a context for the fossil hominins.

### 3.1. Composition of the faunal spectrum

At Malapa, 27 species have been identified so far (Dirks *et al*., 2010; Kuhn *et al*., 2011; Val *et al*., 2011; Hartstone-Rose *et al*., 2013), including the hominins (for a complete list of species, see Chapter 3). Even though the number of species is lower than in larger deposits from the Cradle of Humankind (i.e. Gladysvale, Cooper's D, Swartkrans Members 1-3, Sterkfontein Member 4; Brain, 1981; Berger *et al*., 1993; Watson, 1993; Lacruz *et al*., 2002; de Ruiter, 2003; Kibii, 2004; de Ruiter *et al*., 2009) (Table 5.1), the faunal diversity at Malapa is high given the small size of the sample and the small amount of excavated *in situ* and *ex situ* sediment.

**Table 5.1.** Faunal diversity in different cave deposits from the Cradle of Humankind (microfauna not included).

| Site | Deposit | Species | References |
|---|---|---|---|
| GLADYSVALE | External Deposits (GVED) and chambers | 74 | Berger *et al*., 1993 ; Lacruz *et al*., |
| COOPER'S | D | 64 | de Ruiter *et al*., 2009; Steininger |
| SWARTKRANS | Member 1 (Lower Bank) | 41 | Watson, 1993; de Ruiter, 2003 |
| | Member 1 (Hanging Remnant) | 42 | |
| | Member 2 | 44 | |
| | Member 3 | 57 | |
| STERKFONTEIN | Member 4 | 50 | Brain, 1981; Kibii, 2004 |
| | Jacovec Cave | 29 | Kibii, 2004; Kibii, 2009 |
| | Member 2 | 13 | Pickering *et al*., 2004a |
| | Silberberg Grotto | 8 | |
| KROMDRAAI | A | 45 | Brain, 1981 |
| | B | 25 | |
| **MALAPA** | **-** | **27** | Dirks *et al*., 2010 ; Kuhn *et al.*, 2011 ; |
| GONDOLIN | GDA | 23 | Adams, 2006 |
| | GD2 | 20 | |
| | GD1 | 9 | |
| DRIMOLEN | - | 20 | Keyser *et al*., 2000; O'Regan and |
| MOTSETSE | - | 15 | Berger and Lacruz, 2003 |
| LULECHE | - | 6 | Adams *et al*., 2007b |
| MINNAAR'S | - | 7 | Gommery *et al*., 2012 |

The assemblage is diverse in terms of orders and families present: it contains 14 families of mammals (Table 5.2), representing bovids, suids, equids, carnivores, as well as primates, rodents, microfauna and birds. Hominins make up a large proportion, comprising nearly a quarter of the assemblage in terms of NISP and MNE (Table 5.2). Only

one specimen of non-hominin primate has been recovered so far (i.e. *Papio* sp.). The carnivore family presents the highest diversity in terms of number of different species identified: nine different species, representing all carnivore families (i.e. felids, hyaenids, canids, viverrids and herpestids), have been identified (Kuhn *et al*., 2011; Hartstone-Rose *et al*., 2013). All class-sizes (small, medium-sized and large mammals) are present in the faunal assemblage, representing a minimum number of 41 individuals. The smallest species identified is a microfaunal species (*Elephantulus* sp.; Val *et al*., 2011), while the largest species identified is a bovid (*Connochaetes* sp.). Only the very large mammals (elephantids, hippopotamids and giraffids) are almost absent (i.e. one specimen only is attributed to an unidentified Class V ungulate, UW88-794). The total number of faunal specimens recorded so far is 1324 (including bones, bone fragments, horn core fragments, carapace fragments, teeth and tooth fragments). Amongst these remains, 993 have been assigned to an order or a family and 331 are unidentifiable (Table 5.2). The overall fragmentation ratio is: total NISP/total MNE = 1324/767 = 1.7.

**Table 5.2.** Quantitative data on the faunal material from Malapa to date, with estimates of the NISP, the MNE and the MNI for each order. Molluscs and invertebrates are not considered.

| Order | Family | NISP | MNE | MNI |
|---|---|---|---|---|
| UNGULATES | Bovidae | 362 | 276 | 9 |
| | Suidae | 4 | 4 | 2 |
| | Equidae | 4 | 4 | 1 |
| | Large size ungulate (giraffid?) | 2 | 2 | 1 |
| | Ungulates indet. | 63 | 21 | - |
| | **Total Ungulates** | **435** | **307** | **13** |
| CARNIVORES | Viverridae/Herpestidae | 64 | 64 | 4 |
| | Felidae | 52 | 50 | 5 |
| | Hyaenidae | 30 | 30 | 3 |
| | Canidae | 10 | 10 | 2 |
| | Carnivores indet. | 20 | 19 | - |
| | **Total Carnivores** | **173** | **171** | **14** |
| PRIMATES | Homininae | 263 | 188 | 6 |
| | Cercopithecidae | 3 | 3 | 1 |
| | **Total Primates** | **267** | **191** | **7** |
| RODENTS | Leporidae and rodents indet. | 52 | 51 | 3 |
| MICROFAUNA | Elephantidae and microfauna indet. | 27 | 27 | 2 |
| TESTUDINES | Chelonidae | 16 | 16 | 1 |
| BIRDS | Indet. | 11 | 8 | 2 |
| Unidentified remains | - | 331 | - | - |
| **TOTAL** | | **1324** | **767** | **41** |

## 3.2. General preservation

### *3.2.1. Articulations*

Both persistent (e.g. sacrum-pelvis, sacrum-lumbar vertebrae, ankle, femur-tibia and humerus-radius) and unstable joints (e.g. knee, tarsals and carpals) are preserved in the non-hominin faunal assemblage, either in the form of true articulations or as anatomical proximities. Some interlocking joints, such as the joint humerus-scapula, are preserved in the form of anatomical proximity.

<u>True articulations</u>

Several elements still in articulation have been recovered (Figures 5.7 and 5.8), including two carnivore ankles (UW88-539: a hyaena ankle and UW88-747: a large felid ankle), two bovid feet (UW88-650: two articulated proximal phalanges, two intermediate phalanges, two distal phalanges and two sesamoids; UW88-751 to 756: a metatarsal articulated with a proximal phalanx and four sesamoids), medium-sized bovid phalanges and sesamoid (UW88-528: a intermediate phalanx, a distal phalanx and one sesamoid), other medium-sized bovid phalanges (intermediate phalanx articulated with distal phalanx, no specimen number), equid carpals (UW88-548: an unciform, UW88-549: an accessory metacarpal, and UW88-550: a magnum), a leporid sacrum in articulation with the last three lumbar vertebrae (specimen UW88-769), nine bovid thoracic vertebrae (two from block UW88-B081, seen using Avizo, and seven on the surface of block UW88-B375), several bovid limb bones (specimen UW88: a femur articulated with a tibia in block UW88-B848, and a humerus articulated with a radio-ulna in block UW88-B051), a near complete bovid foetus, in articulation (preserved in block) and some articulated limb bones (specimen UW88-687: taxon indeterminate) (Figures 5.7 and 5.8).

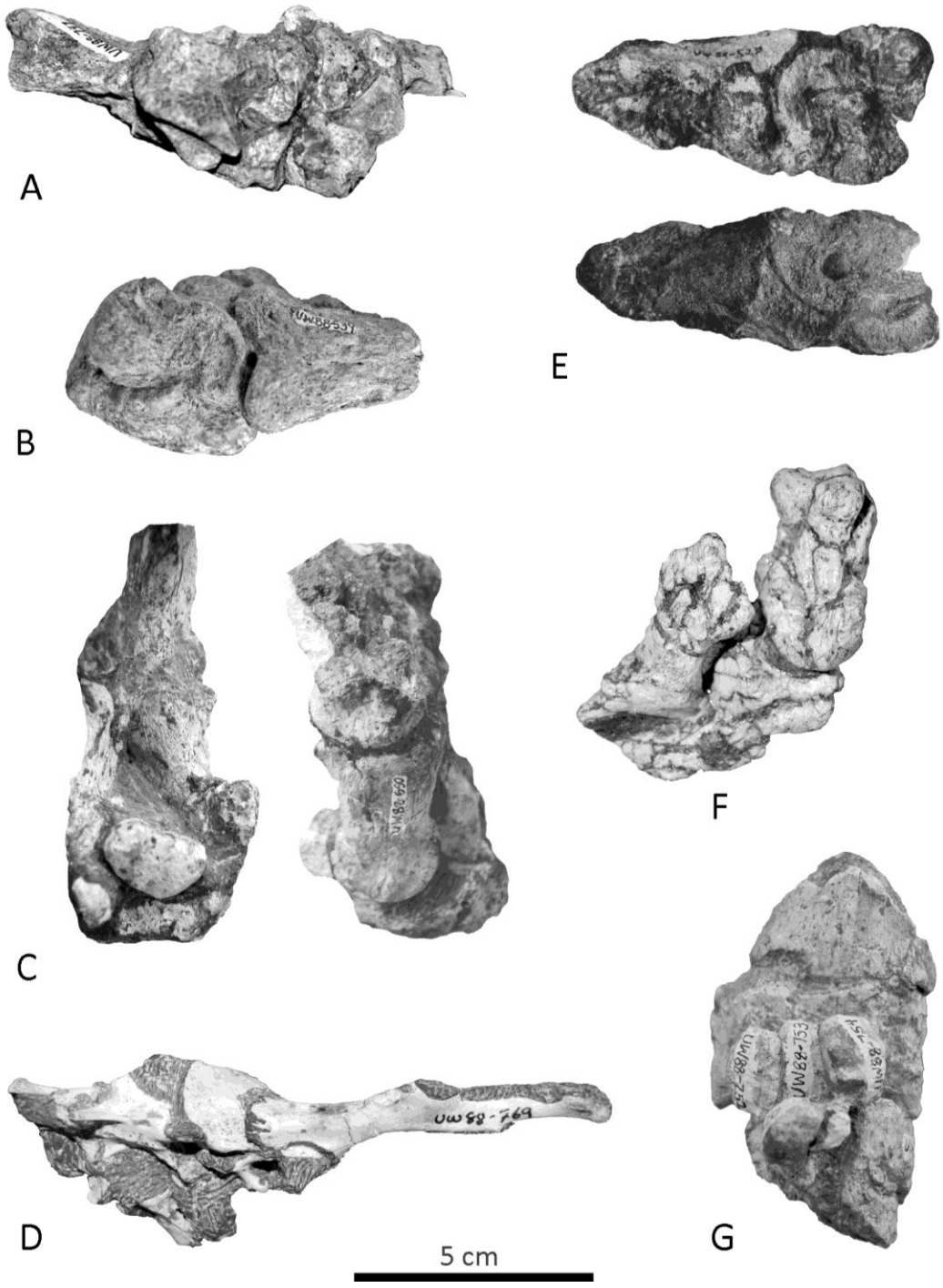



**Figure 5.7**. Examples of articulated non-hominin faunal remains. A: specimen UW88-747, *Dinofelis* sp. articulated right ankle; B: specimen UW88-739, *P. brunnea* articulated ankle; C: UW88-650, bovid articulated foot; D: specimen UW88-769, rabbit pelvis articulated with the sacrum and the last lumbar vertebrae; E: specimen UW88-528, bovid articulated intermediate and distal phalanges and one sesamoid; F: no specimen number, bovid intermediate and distal phalanges; G: specimens UW88-751-756, bovid metatarsal, first phalanx and sesamoids.

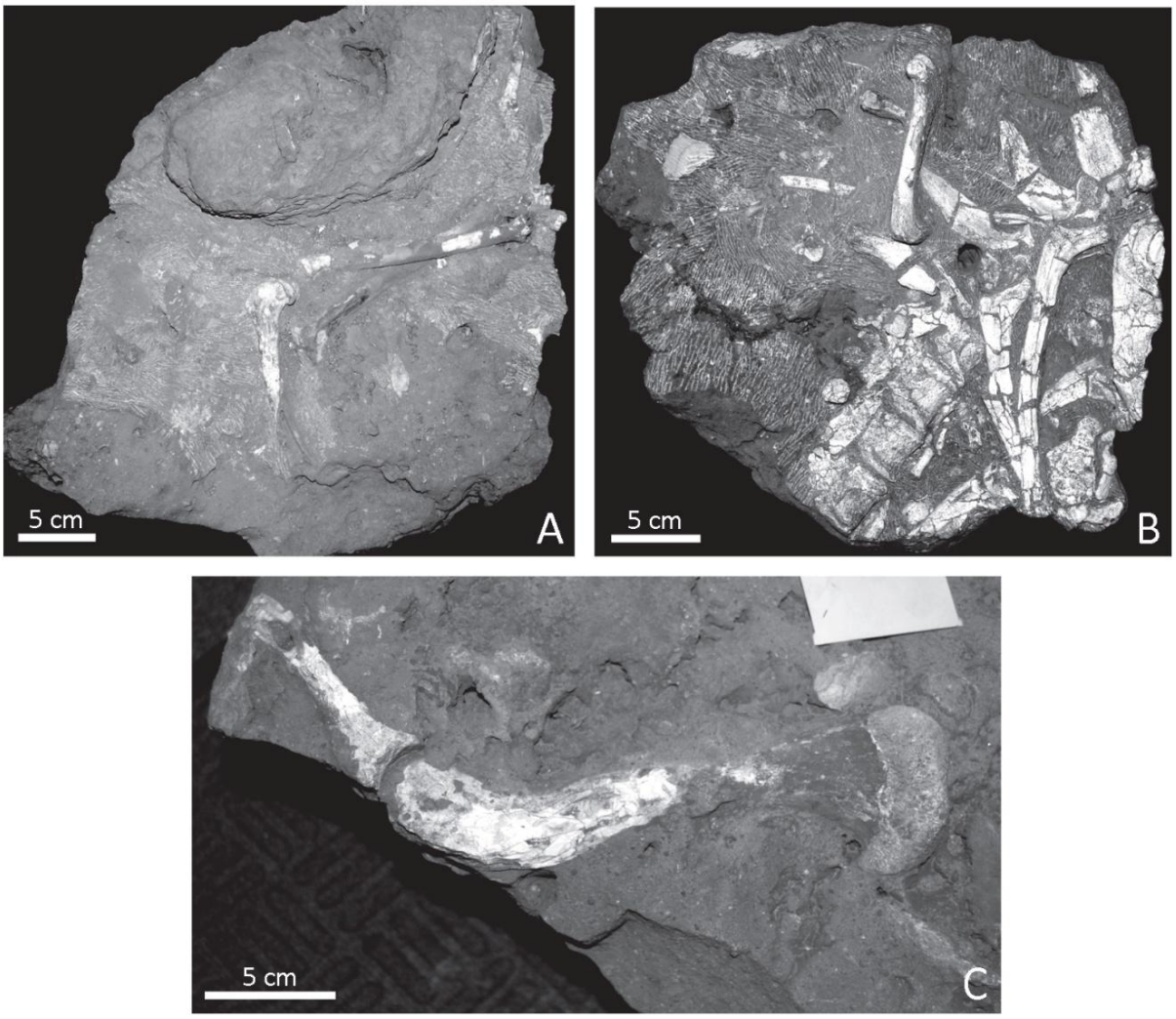



**Figure 5.8**. Examples of articulated non-hominin faunal remains in blocks. A: one bovid femur, two tibiae, and one talus in block UW88-B848; B: bovid thoracic vertebrae associated with bovid ribs, one humerus and an ungulate mandible with teeth, in block UW88-B375; C: bovid humerus articulated with a radio-ulna, in block UW88-B051.

## Anatomical proximities

Other remains have been recovered in close proximity to one another (Figures 5.9 and 5.10), for instance a near articulated bovid left ankle (UW88-1156 to 1160: talus, calcaneum, lateral malleolus, cuneiform and cubo-navicular), large bovid carpals (UW88-1259a, b and c: fragmentary scaphoid, hamate and possible magnum), a rodent skull and associated mandible (specimen UW88-781), two hyaenid phalanges (UW88-782: a

proximal phalanx, and UW88-783: an intermediate phalanx), some small mammal lumbar vertebrae (no specimen number), a bovid humerus and scapula (still embedded in block UW88-B243), some bovid ribs (in blocks UW88-B375 and UW88-B152), two bovid cervical vertebrae (UW88-720 and UW88-721), three bovid cervical vertebrae still embedded in a block of calcified sediment (UW88-B199: an atlas, axis and third cervical), two ribs and a thoracic vertebra of a bovid (no specimen number), elements of a left lower limb of a bovid (left tibia, metatarsal, talus and cubo-navicual, in block UW88-848) and unidentified mammal ribs (still embedded in block UW88-1043), a partial bovid foetus, in near articulation (preserved in block and currently under preparation), and a complete upper body of a small carnivore , of similar size and morphology of a small spotted genet (*Genetta genetta*), still under preparation (no specimen number, including a hemi-mandible, a left zygomatic and associated teeth, the right and left humeri, a right scapula, radius and ulna, four right metacarpals, from rank II to V, two carpals, ten ribs, ten thoracic vertebrae, six lumbar vertebrae and a sacrum) (Figures 5.9 and 5.10).

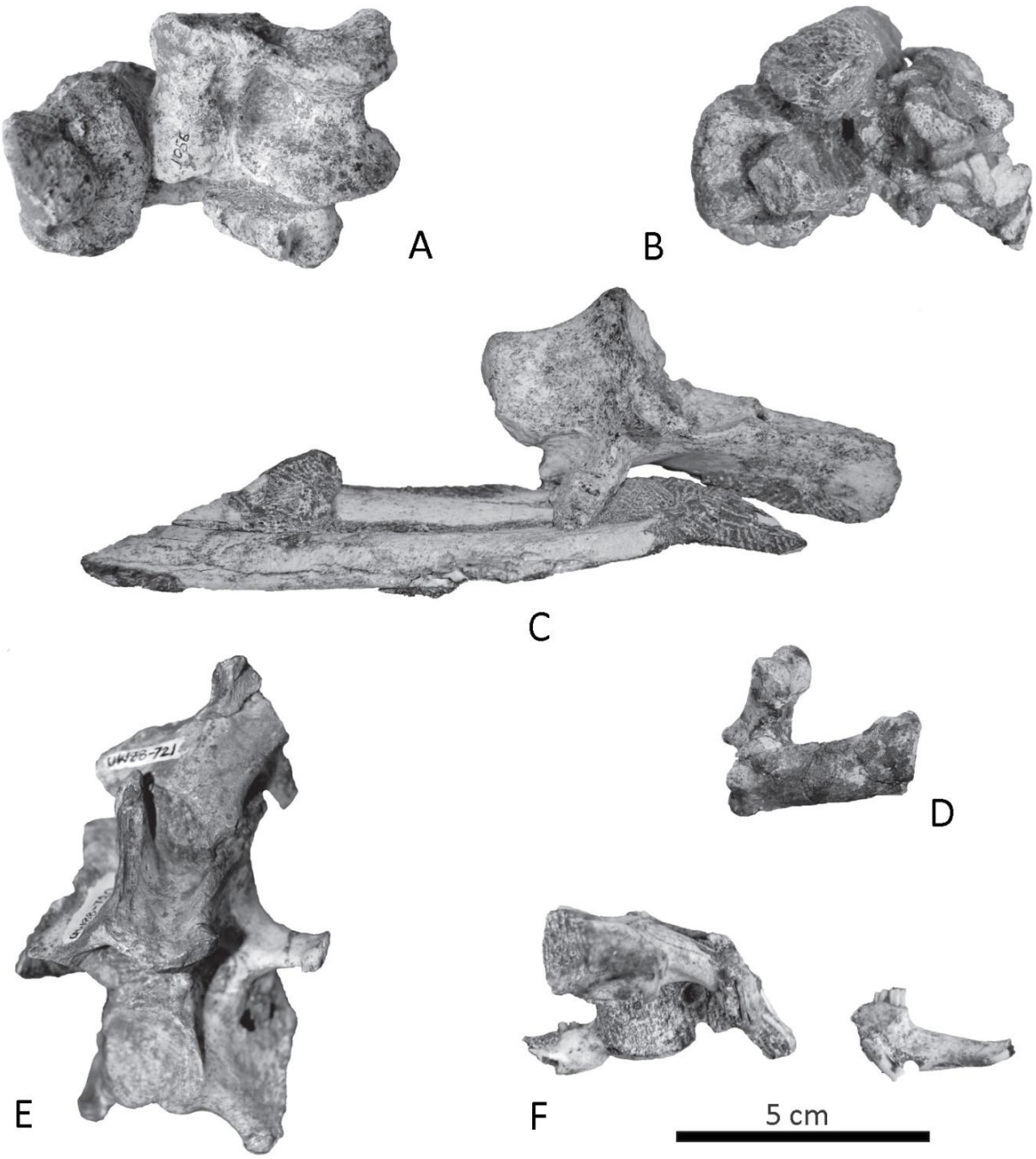



**Figure 5.9**. Examples of non-hominin faunal remains in anatomical proximity. A: specimens UW88-1156 to 1160, bovid left ankle; B: specimens UW88-1259a to 1259c, large bovid carpals; C: specimens UW88-720-722, bovid atlas, axis and third cervical vertebra; D: specimens UW88-782 and 783, hyaenid phalanges; E: no specimen number, bovid ribs articulated with a thoracic vertebra; F: specimen UW88-781, rodent skull and associated mandible.

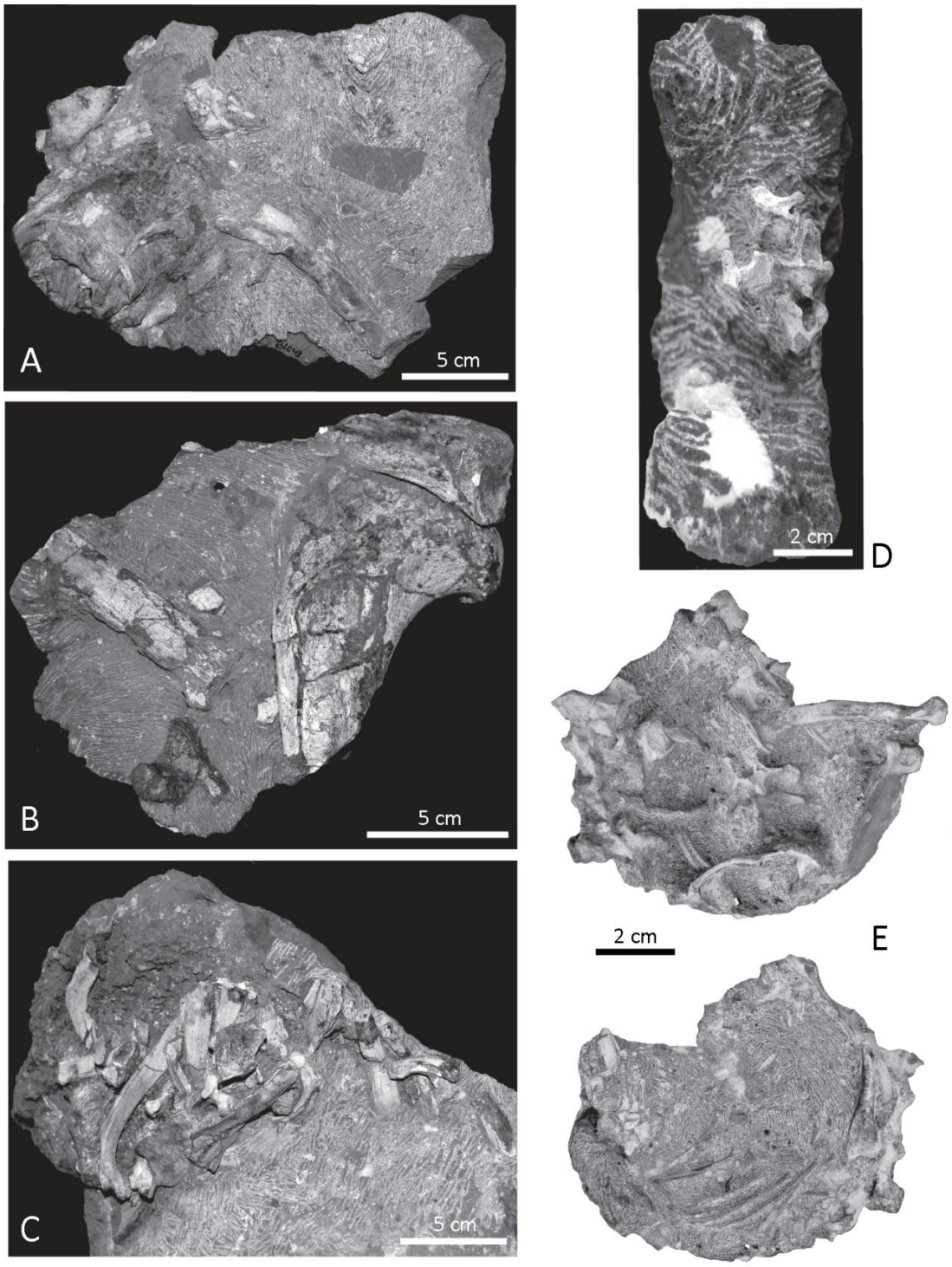



**Figure 5.10.** Examples of non-hominin faunal remains in near articulation, still embedded in calcified sediment. A: mammal ribs in block UW88-B1043; B: bovid humerus and associated scapula in block UW88-B243; C: bovid ribs in block UW88-B152; D: small mammal lumbar vertebrae, no specimen number; E: superior and inferior views of the same block containing the bones of a small carnivore skeleton, no specimen number.

### *3.2.2. Complete and near complete bones*

Abundant complete and near complete bones occur in the assemblage. For the bovids, the number (NISP) of complete bones is 103; the number of near complete bones is 20 and the number of fragmented bones is 213. The complete elements are mostly carpals, tarsals, phalanges and vertebrae. For the carnivores, the number of complete bones is 83, the number of near complete bones is five and the number of fragmented bones is 83. The complete elements are mostly carpals, tarsals, phalanges, teeth and vertebrae. It is worth noting that the presence in the carnivore assemblage of an extremely well preserved skeleton of a small carnivore (Figure 5.10) contributes greatly to increase the number of complete bones. Other species that are also preserved as complete bones include two complete equid carpals (out of four bones); a complete phalanx and a complete metapodial of suid (out of four bones); four complete and three near complete leporid bones (out of 31), including a femur, an innominate, a sacrum, a tibia, two hemi-mandibles and a lumbar vertebra, most likely belonging to the same individual.

### *3.2.3. Antimeric sets of bones*

At least twelve antimeric sets of bones (long bones and mandibles) are present (see Appendix 4 for the complete list). They represent a minimum of five animals, including one leporid, one felid, and three bovids.

### *3.2.4. Representation of skeletal elements*

All parts of the skeleton are present in the non-hominin faunal assemblage, in different proportions: long bones and flat bones, phalanges, metapodials and carpals/tarsals, ribs and vertebrae, crania and teeth. The pattern of survival seems to be generally consistent with a density-mediated preservation pattern, whereby all elements are present in various proportions related to differential conservation. Hence, dense and compact bones, such as long bone shafts, mandibles and metapodials (Lyman, 1984;

Binford and Bertram, 1977; Kreutzer, 1992; Lam *et al*., 1998, 1999; Novecosky and Popkin, 2005), dominate the assemblage, followed by elements with a lesser density, such as phalanges, scapulae and pelvises. Fragile elements with a low density, such as vertebrae and ribs (Lyman, 1984; Binford and Bertram, 1977; Kreutzer, 1992; Lam *et al*., 1998, 1999; Novecosky and Popkin, 2005) are underrepresented (Figure 5.11 and Appendix 5). However, biases due to selection and preparation can also explain the higher representation of denser elements. The more compact the bones are, the more they have a chance to be preserved complete or near complete, and therefore to be more easily identified and prioritized for preparation. Since the provenance of most fossils is unknown, the body part representation may also vary from one facies to the other. Thus, the density-mediated pattern of bone survival does not necessarily apply to all fossil-bearing units.

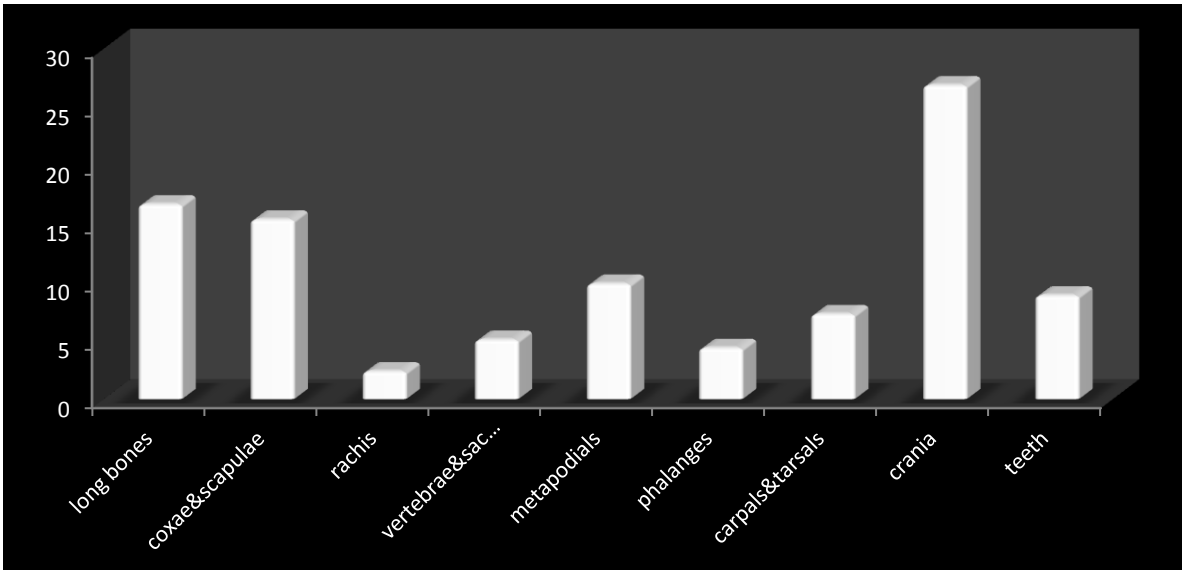



**Figure 5.11**. Percentages of survival for each body part for the non-hominin faunal assemblage (ungulates and carnivores).

## 3.3. Modifications of the bone

### *3.3.1. Modifications by abiotic agents*

Weathering

The non-hominin assemblage is extremely heterogeneous in terms of bone weathering: bones showing all stages are present, from non-weathered (stage 1) to highly-weathered (stage 5; Table 5.3). Stages 2 to 4 are present in fairly similar proportions; the less weathered remains represent the majority of the assemblage, and the most weathered remains only a small percentage (5.4%) (Table 5.3). The majority of the fossils available shows little weathering (Table 5.3), with only superficial cracks on the bone surface.

**Table 5.3.** Weathering stages observed in the non-hominin faunal assemblage.

| Stage | No. of specimens | % |
|---|---|---|
| **1** | 243 | 34.4 |
| **2** | 170 | 24.0 |
| **3** | 127 | 18.0 |
| **4** | 129 | 18.2 |
| **5** | 38 | 5.4 |

Manganese precipitation

Six stages in the extent of precipitated manganese dioxide on the bone surface are observed: none, slight (only a few spots), slight to moderate (abundant spots), moderate (half the surface of the specimen is covered), moderate to heavy (the majority of the bone surface is covered with small patches visible), and heavy (the whole surface of the specimen is covered) (Figure 5.12).

**Figure 5.12**. Different degrees of manganese covering observed on the bones (from left to right: slight, slight to moderate, moderate, moderate to heavy, and heavy).

The majority of the bones analysed (*n.* 657, or 77.8%) show manganese precipitate on their surface, and most of the remains exhibit a layer of manganese falling in categories "slightly" and "moderate" (Table 5.4).

**Table 5.4**. Extent of the manganese dioxide perimineralization on the non-hominin bone surfaces.

| Degree | No. of specimens |
|---|---|
| absent | 59 |
| slight | 327 |
| slight to moderate | 37 |
| moderate | 175 |
| moderate to heavy | 83 |
| heavy | 35 |

There is a clear difference between fossil bones found in calcified sediment and those found in decalcified sediment in terms of manganese covering. The bones from decalcified deposits are commonly heavily coated with manganese crust, whereas remains from calcified sediment have much less manganese on their surface (Table 5.5 and Figure 5.13).

**Table 5.5.** Comparison of degree of manganese dioxide coating according to the provenance of the remains (decalcified versus calcified sediment).

| Degree | Bones found in decalcified sediment | Bones found in calcified sediment |
|---|---|---|
| absent | 7 | 46 |
| slight | 82 | 171 |
| slight to moderate | 17 | 17 |
| moderate | 126 | 48 |
| moderate to heavy | 79 | 2 |
| heavy | 29 | 4 |

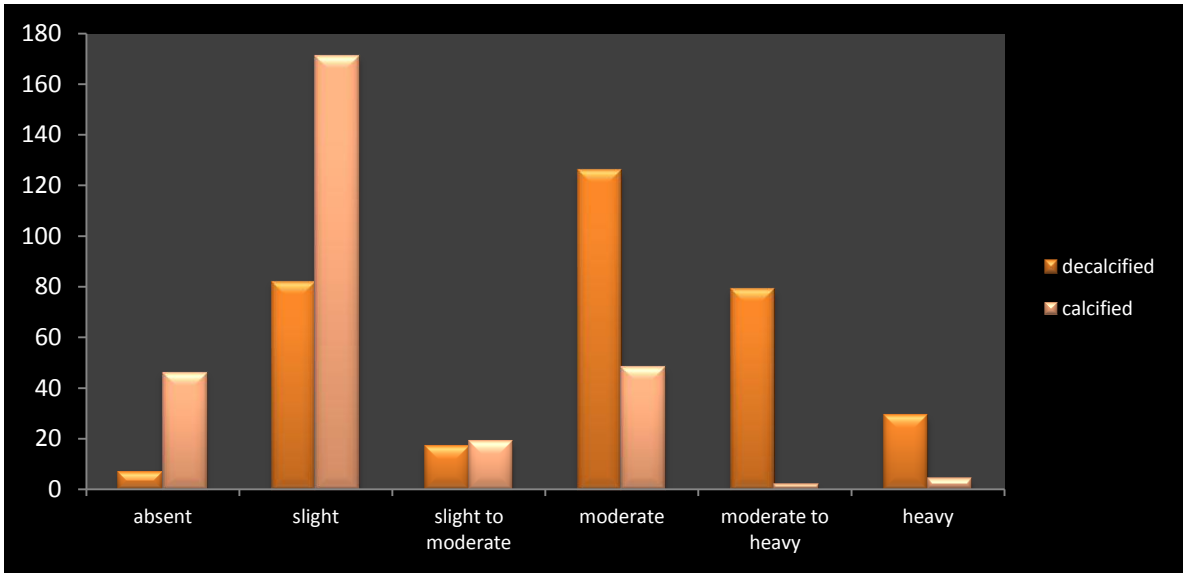



**Figure 5.13.** Comparison of degree of manganese dioxide perimineralization according to the provenance of the remains (decalcified sediment, in orange, versus calcified sediment, in light pink).

## Calcite crystal growth

Crystals of calcite are very abundant; they have been recorded on 29.7% (*n.* 315) of the non-hominin assemblage, and occur in three forms: inside spongy bone, in cracks on compact bone and in the medullary cavity of long bones and ribs (Figure 5.14). Calcite crystals are mostly present on remains recovered in calcified sediment (*n.* 278 from calcified sediment and *n.* 37 from decalcified sediment).

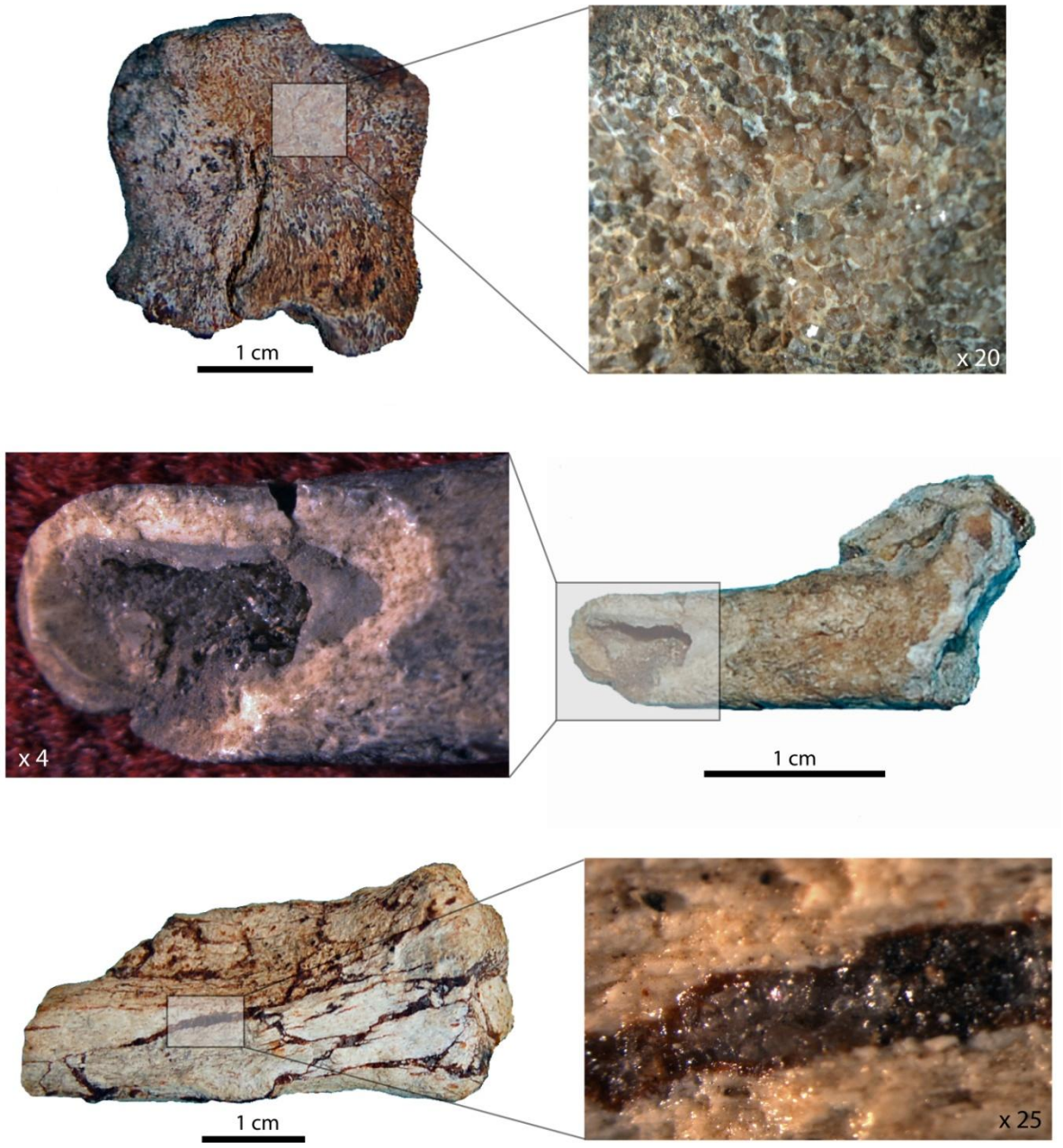



**Figure 5.14**. Different types of calcite crystal growth in non-hominin bones. Top: inside spongy bone; middle: inside the medullary cavity, and bottom: inside cracks in cortical bone.

Red colour staining

Red (colour varying between orangey and dark red) traces are visible on numerous remains (*n.* 392, representing 36.9% of the analysed non-hominin faunal assemblage) and consist of very thin reddish patches covering parts of the bones (Figure 5.15). The origin of

these traces is currently under study (Keeling, unpublished MSc dissertation), testing the hypothesis that they could be organic in nature.


**Figure 5.15.** Examples of red traces at macro- and microscopic level on different bones.

Sedimentary compaction

The pressure exerted on buried bones by the continual built-up of sediments has led to the flattening and, in some cases, the distortion of the fossils (Figure 5.16). Compressional effect of sediments can be observed on 44 remains, representing 5.4% of the analysed non-hominin assemblage.

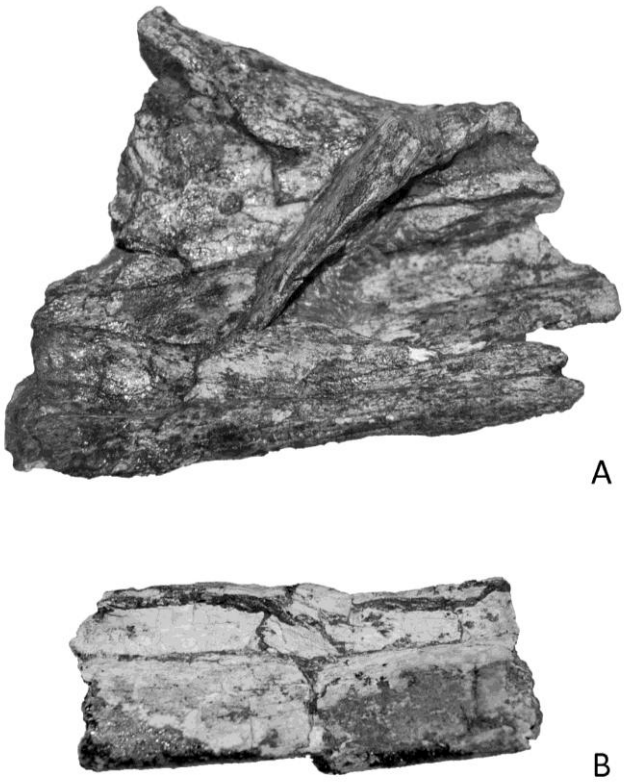



**Figure 5.16.** Examples of specimens distorted by overburden pressure. A: bovid scapula (UW88-1266); B: unidentified rib fragment from block UW88-B808 (no specimen number).

Decalcification

Some remains (*n.* 149, or 18.9% of the analysed non-hominin faunal assemblage) have undergone a partial or complete decalcification process (i.e. the calcium originally present in the bone has disappeared), which leads to a loss of colour and the bones becoming very white. Decalcification is equally common amongst specimens recovered in decalcified sediment (*n.* 69), and in calcified sediment (*n.* 72).

### *3.3.2. Modifications by biotic agents*

Trampling

Trampling has had a minor impact as only 22 bones show definitive trample marks, representing 2.7% of the analysed non-hominin faunal assemblage. Trample marks are isolated and of microscopic dimensions (i.e. visible using low magnification). They are observed in relatively equal proportions on remains recovered from calcified (*n.* 14) and decalcified sediment (*n.* 8), which indicates that it took place prior to burial and fossilisation, either outside the cave or in an area of the cave system accessible to the large hoofed animals.

Root growth

Damage produced by roots and/or rootlets is almost non-existent in the non-hominin faunal assemblage. Only four bovid remains, including one tooth fragment recovered *in situ* and three bone fragments recovered in *ex situ* calcified sediment, show microscopic modifications in the form of branched network of small grooves, which may be attributed to vegetal action.

Carnivore damage

Only two specimens (UW88-878, a bovid rib fragment, and UW88-1017, an unidentified long bone shaft fragment) exhibit some evidence of pitting produced by a mammalian carnivore (Figure 5.17). The pits on specimen UW88-878 are between 0.9 and 3.5 mm in length and between 0.4 and 0.8 mm in breadth, with an average length of 1.4 mm and an average breadth of 0.6 mm. They fall therefore in the range of pits produced by small carnivores (e.g. wild cat, mongoose, jackal) and middle size felids (e.g. leopard and cheetah) (Selvaggio and Wilder, 2001; Domínguez-Rodrigo and Piqueras, 2003). Nevertheless, on average, they are smaller than pits produced by leopards, which have an average length and breadth of 2 mm and 1 mm respectively (Domínguez-Rodrigo and

Piqueras, 2003). The pit observed on the long bone fragment is larger (4 mm in length and 3.5 mm in breadth) and fall in the range of pits produced by large carnivores (lions and spotted hyaenas; Selvaggio and Wilder, 2001; Domínguez-Rodrigo and Piqueras, 2003). Twenty-three long bones and metapodials of medium and large size mammals are preserved in the form of cylindrical shafts (i.e. the complete circumference of the shaft is preserved with or without one extremity). However, the breakage pattern is in most cases consistent with a fracture happening once the bones had already weathered. Furthermore, fresh breakage is never associated with any evidence of carnivore tooth damage and cannot be directly attributed to carnivore action. There is no evidence of digested bone.


**Figure 5.17.** Carnivore pitting on a bovid rib shaft fragment (specimen UW88-878).

Rodent damage

There is no evidence for rodent chewing or gnawing damage; no rodent tooth marks have been recorded.

Bird of prey damage

None of the bones show evidence of damage by a bird of prey (no digested bone, no impact of beak or talons). The presence of some microfauna in the deposit could indicate a possible but minor contribution to the assemblage by owls.

Invertebrate damage

Two types of invertebrate modifications, of different size and morphology, consistent with two different arthropod agents, are recorded. Type 1 is only present on two remains and consists of a large boring (i.e. large hole associated with an elongate furrow; Figure 5.18). Similar features have been observed in the faunal assemblage from nearby Cooper's D cave (C. Steininger, pers. comm.). The identity of the species causing this type of damage is unknown.

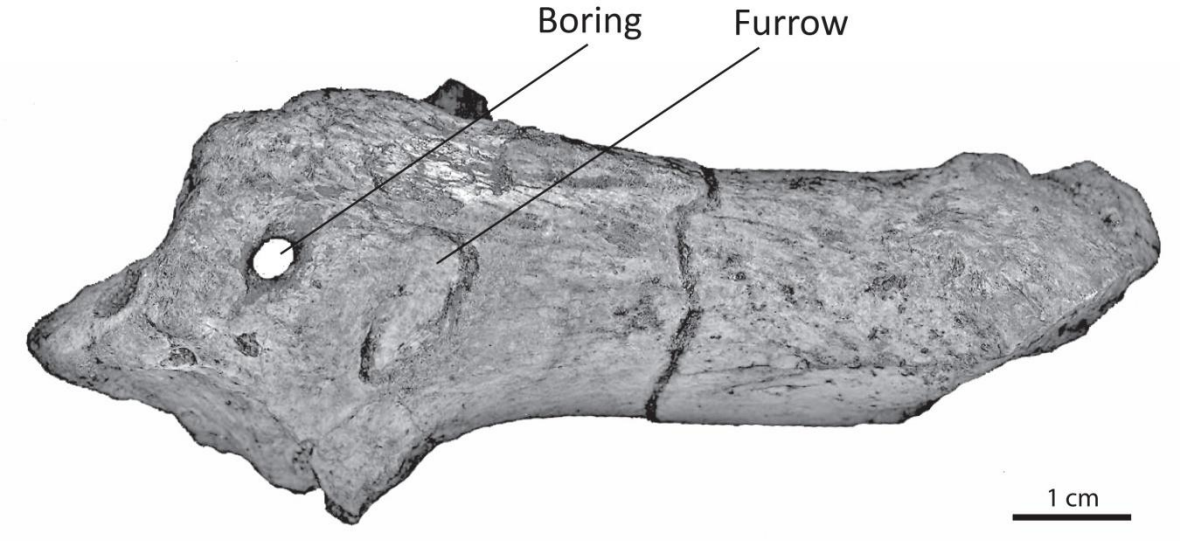



**Figure 5.18.** Invertebrate modification type 1 (boring and associated furrow) on a bovid calcaneum.

Type 2 (Figure 5.19) modifications have been recorded on 115 remains, or 13% of the analysed non-hominin faunal material. Preliminary comparisons with experimentally produced invertebrate damage and data from the literature (see Chapter 4) suggest that the type 2 modifications observed on the Malapa non-hominin faunal material may have been produced by invertebrates belonging to the Order Coleoptera (hide beetles, *Omorgus squalidus*) or to the Order Isoptera (termites). However, it is uncertain at this stage whether the traces were made by one or more agents, as they take variable forms: intersecting striations, parallel striations, pits containing intersecting striations on the bottom, star pits (i.e. pits with scratches arranged around the pit in a star-shape manner) and furrows associated with boring (Figure 5.19).

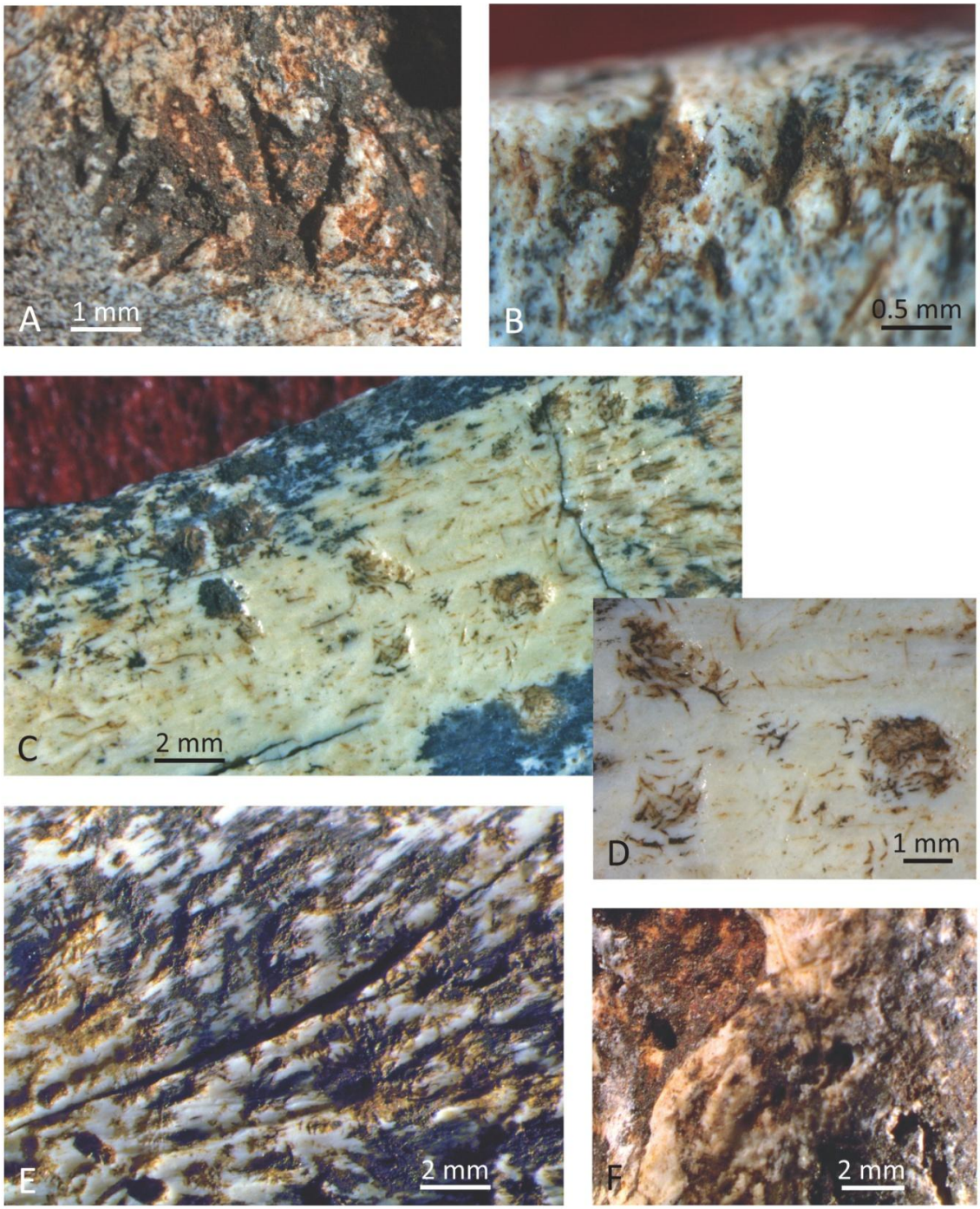



**Figure 5.19**. Different types of invertebrate damage of type 2 observed on the non-hominin faunal remains. A: deep intersecting striations; B: similar, more parallel striations; C: intersecting striations associated with pits; D: same as C, close-up; E: star-shaped pits; and F: small boreholes.

The majority of modifications of type 2 are located on bone and tooth fragments recovered from decalcified sediment (Table 5.6 and Figure 5.20). They are concentrated on compact bone and commonly occur on the edge of the fragments. The most common features exhibited on the bones are the intersecting traces, which are sometimes associated with a pit (Figures 5.19, 5.20 and Table 5.6). Most of the type 2 traces occur beneath the manganese crust, indicating that they were made prior to the precipitation of manganese on the bones.

**Table 5.6.** Invertebrate modifications of type 2 observed on the fossil remains, according to the provenance of the remains (decalcified versus calcified sediment).

| Modifications | Bones from decalcified sediment | Bones from calcified sediment |
|---|---|---|
| Intersecting striations | 80 | 4 |
| Parallel striations | 12 | 1 |
| Pits with intersecting striations | 54 | 3 |
| Star-shaped pits | 3 | 1 |
| Small borings | 23 | 9 |
| Total remains | 99 | 13 |

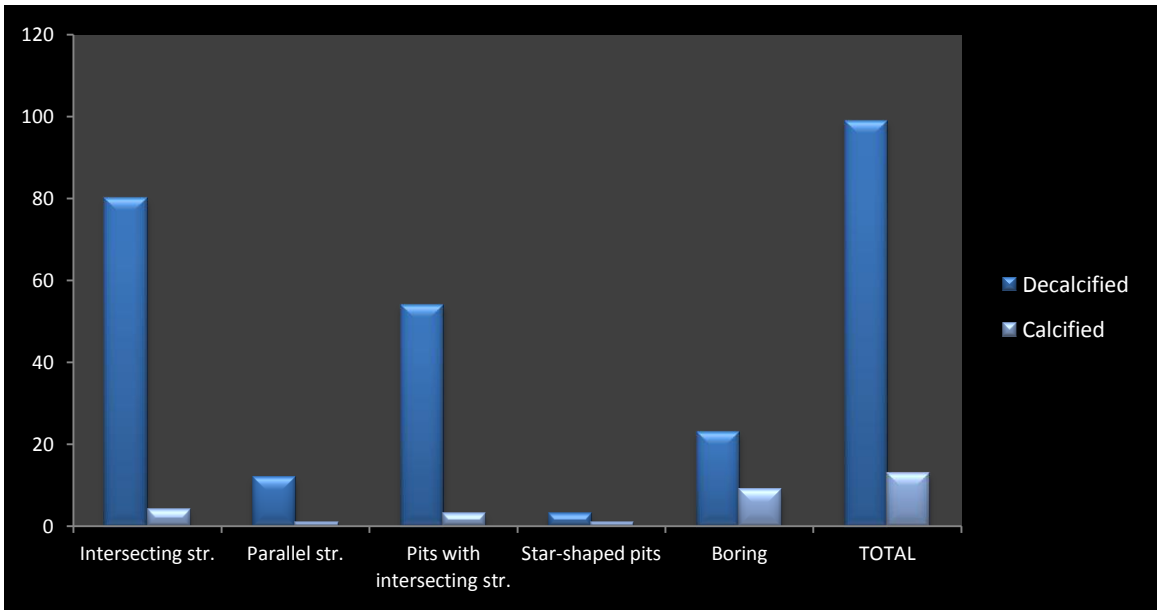



**Figure 5.20**. Distribution of the invertebrate modifications (type 2) according to the provenance of the remains (decalcified versus calcified sediment) (str. = striations).

The invertebrate modifications are mostly present on weathered remains, between stages 2 and 5 (Table 5.7 and Figure 5.21). The high number of weathered bones with insect damage indicates that invertebrate action on the bones took place after all or most of the soft tissue (e.g. meat, ligaments, tendons, and marrow) had shrivelled or disappeared. Together with the fact that most modifications occur on bones recovered from decalcified sediment, it seems that the insect modifications were made after the bones were already fossils.

**Table.5.7.** Invertebrate damage, according to the weathering stage of the fossils.

| Number of remains with invertebrate damage | Weathering stage |
|---|---|
| 14 | 1 |
| 31 | 2 |
| 13 | 3 |
| 40 | 4 |
| 9 | 5 |

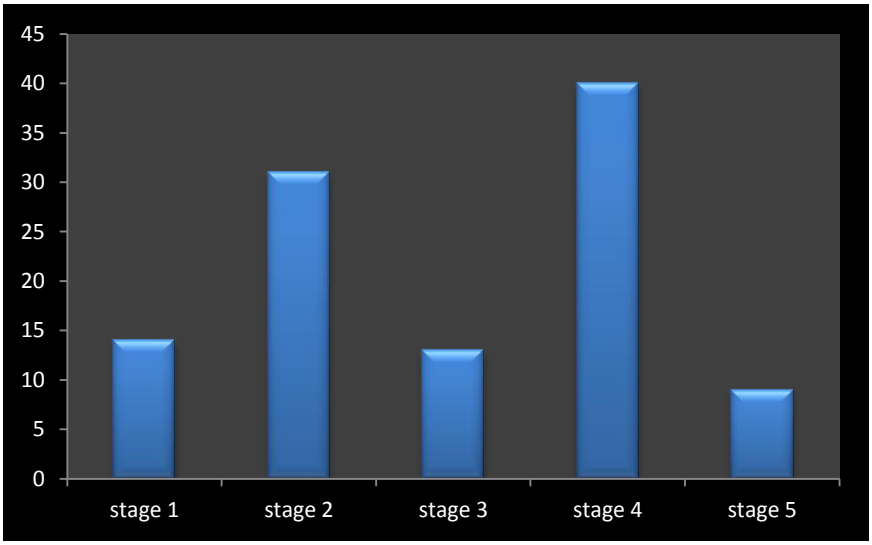



**Figure 5.21**. Distribution of the remains bearing invertebrate damage according to weathering stage.

Ancient anthropogenic damage

No unequivocal cut mark produced by a stone-tool has been observed and no burnt bone has been identified in the assemblage.

### 3.4. Non-hominin faunal material: summary about the state of preservation

The degree of preservation of the faunal material is heterogeneous, ranging from fossils that are very well-preserved, complete, articulated, with little weathering and manganese coating, to fossils that are extremely poorly preserved, fragmentary, highly weathered and covered with manganese dioxide (Figure 5.22).

The different host rocks of the specimens (e.g. calcified versus decalcified sediment; various facies) can partly explain this heterogeneity. The hominins are not the only individuals at Malapa to be very well preserved, since other animals present an excellent state of preservation, as illustrated by the abundance of elements that are articulated or in near articulation, of complete and near complete bones, and by the presence of antimeric sets of bones. These well-preserved specimens are also characterised by a bone surface showing slight weathering, little manganese coating and no carnivore or rodent damage. Based on the number of antimeric sets of bones, articulated elements, complete and near complete bones, it is possible to propose an estimation of a minimum number of five individuals preserved as complete or near complete skeletons in the deposit, including three bovids, one rabbit, and one small carnivore (see Appendix 6 for a detailed list).

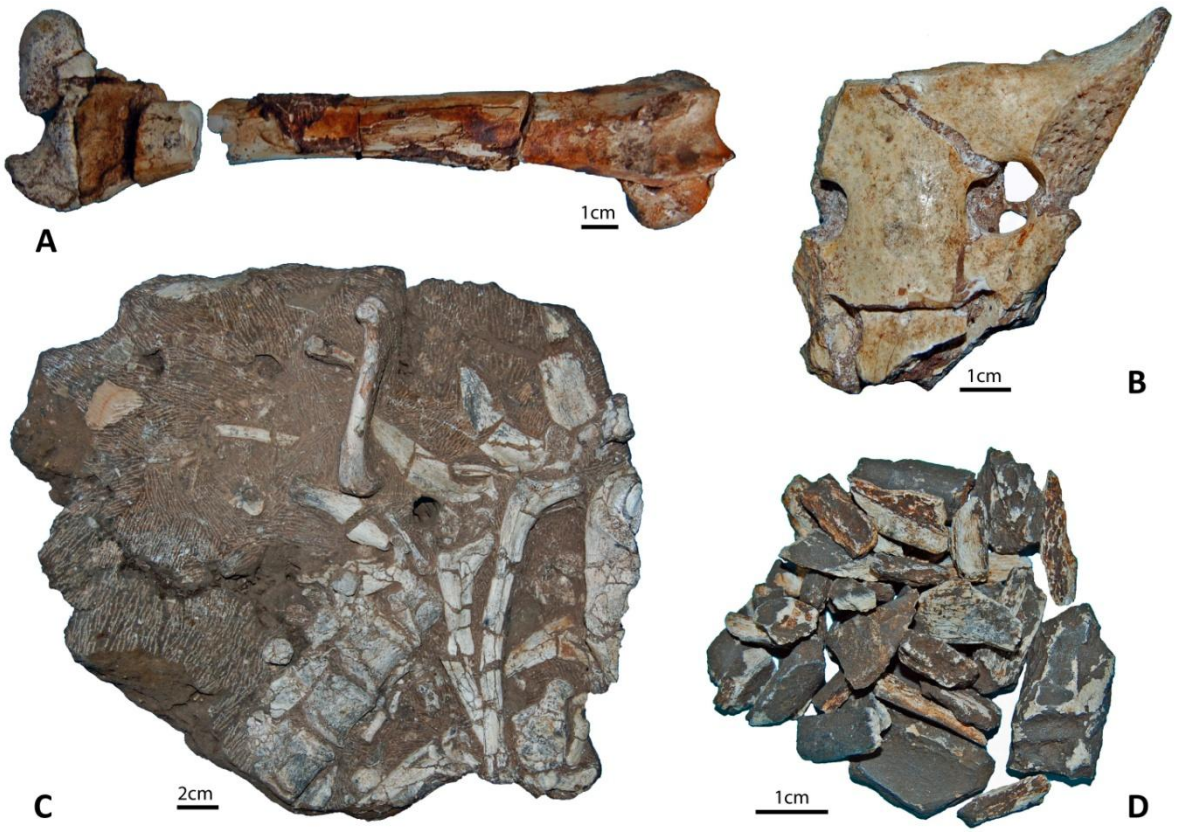



**Figure 5.22.** Heterogeneity of the faunal material; A: highly weathered and decalcified bovid femur; B: non-weathered, well-preserved bovid sacrum; C: articulated bovid ribs and thoracic vertebrae; D: extremely fragmentary unidentifiable bones covered with manganese.

# Chapter 6. State of preservation of the hominins

This chapter presents the results of the palaeontological and physical taphonomic analyses of the MH1 and MH2 skeletons. Firstly, information about the general state of preservation is provided, including degree of survival of body parts, level of completeness, intensity of fragmentation and types of articulations preserved. Secondly, results of the macro- and microscopic study of the bone surfaces are presented, together with the identification of the biotic and abiotic agents that have caused modifications. Finally, a comparison between both individuals allows a discussion of the similarities and differences between them, in terms of their taphonomic characteristics.

## 1. DEGREE OF COMPLETENESS

### 1.1. Percentage survival

The MH2 and MH1 skeletons preserve most body parts. Table 6.1 and Figure 6.1 illustrate which skeletal elements of both MH1 and MH2 have been recovered. For MH1, the total number of bones includes all the bones coming from the yet unprepared block of calcified sediment. The ones for which a definitive identification is required only appear in the total and not in the previous lines (this applies to the five hand or foot bones, the possible tibia/distal femur and the possible humeral shaft elements).

The overall percentage survival is 34% for MH1 and 45.6% for MH2. It is interesting to notice that excluding the very small elements (phalanges, metapodials and carpals/tarsals), the percentage survival for MH1 and MH2 is *exactly* the same: 59.6%.

**Table 6.1.** Percentage survival of each element per individual.

| Element | N | MH1 | | | MH2 | | |
|---|---|---|---|---|---|---|---|
| | | NISP | MNE | % survival | NISP | MNE | % survival |
| Skull | 1 | 3 | 1 | **100** | 0 | 0 | **0** |
| Hemi-mandible | 2 | 3 | 2 | **100** | 5 | 2 | **100** |
| Teeth | 32 | 19 | 16 | **50** | 12 | 12 | **37.5** |
| Clavicle | 2 | 4 | 2 | **100** | 3 | 2 | **100** |
| Sternum | 1 | 1 | 1 | **100** | 1 | 1 | **100** |
| Ribs | 26 | 14 | 10 | **38.5** | 24 | 13 | **50** |
| Cervical vertebrae | 6 | 5 | 5 | **83.3** | 2 | 2 | **33.3** |
| Thoracic vertebrae | 12 | 5 | 4 | **41.7** | 7 | 7 | **58.3** |
| Lumbar vertebrae | 7 | 2 | 2 | **28.6** | 4 | 2 | **28.6** |
| Total vertebrae | 25 | 12 | 12 | **48** | 14 | 11 | **44** |
| Sacrum | 1 | 0 | 0 | **0** | 2 | 1 | **100** |
| Pelvic bone | 2 | 4 | 2 | **100** | 6 | 2 | **100** |
| Humerus | 2 | 4 | 2 | **100** | 2 | 2 | **100** |
| Radius | 2 | 4 | 2 | **100** | 1 | 1 | **50** |
| Ulna | 2 | 3 | 1 | **50** | 1 | 1 | **50** |
| Carpals | 14 | 0 | 0 | **0** | 8 | 8 | **57.1** |
| Metacarpals | 10 | 1 | 1 | **10** | 6 | 6 | **60** |
| Femur | 2 | 5 | 2 | **100** | 4 | 2 | **100** |
| Patella | 2 | 0 | 0 | **0** | 2 | 1 | **50** |
| Tibia | 2 | 0 | 0 | **50** | 4 | 2 | **100** |
| Fibula | 2 | 1 | 1 | **50** | 5 | ½? | **50/100?** |
| Tarsals | 12 | 0 | 0 | **41.7** | 2 | 2 | **16.7** |
| Metatarsals | 10 | 2 | 2 | **20** | 0 | 0 | **0** |
| Phalanges | 42 | 0 | 0 | **0** | 11 | 11 | **26.2** |
| **TOTAL** | 182 | 101 | 62 | **34** | 128 | 83 | **45.6** |

*N: number of elements in a complete skeleton, NISP: Number of Identified Specimens, MNE: Minimum Number of Elements.*

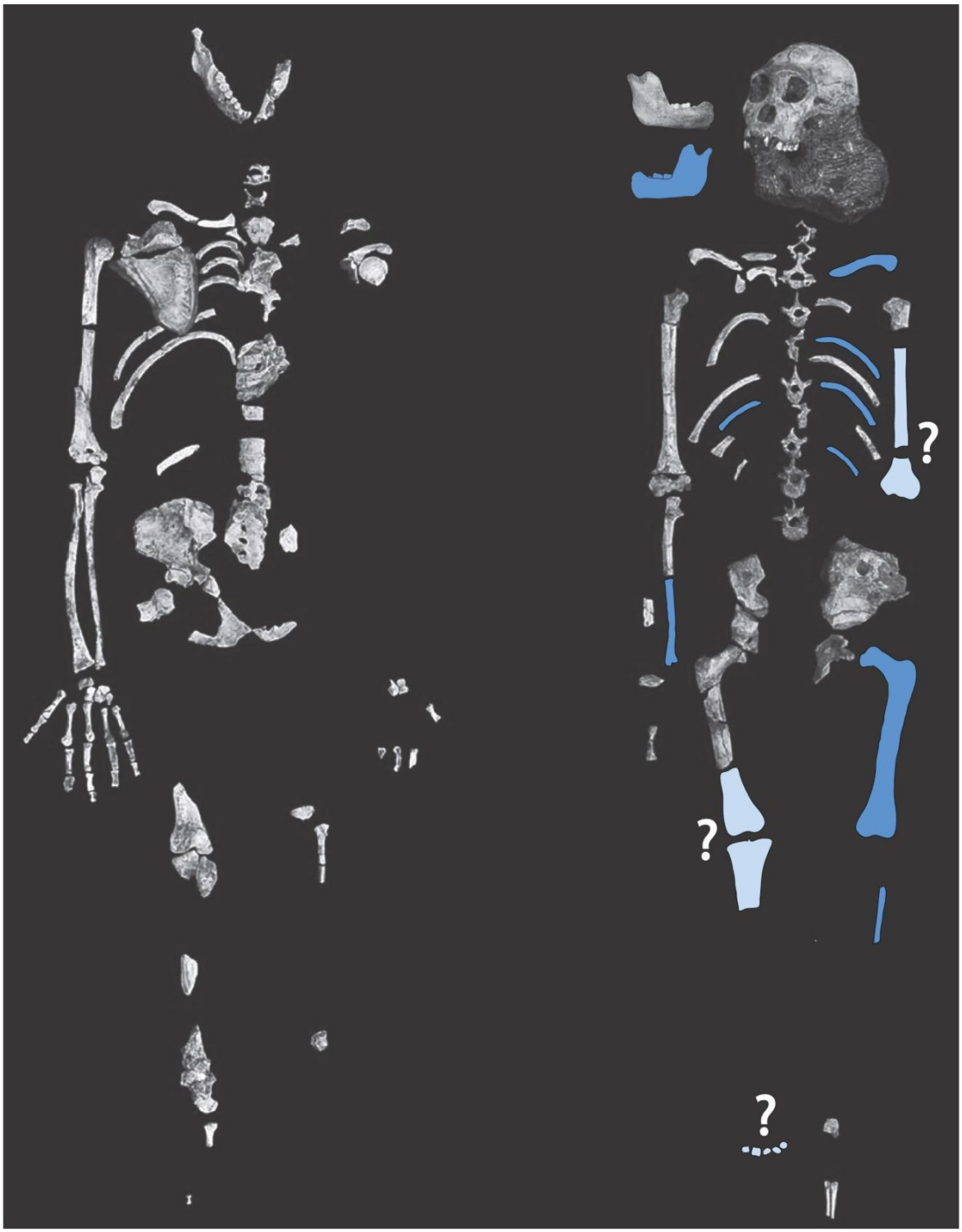



**Figure 6.1.** Remains of MH2 (left) and MH1 (right). The bones in blue are the ones identified in an unprepared block (UW88-B051) and attributed to MH1 (dark blue: anatomical identification certain; bones in light blue: anatomical identification uncertain). Modified from Berger, 2012.

### *1.1.1. MH1*

MH1 has an overall percentage survival (see p.66, Chapter 4, section 2.2.1 for the definition of percentage survival) of: 100 x MNE/182 (where 182 is the total number of elements in an australopithecine skeleton) = (100 x62)/182 = 35.2%. All the major segments of the skeleton are present: skull and teeth, mandible, forelimbs and hind limbs, elements of the hands and the feet, axial skeleton and pelvis (Table 6.1; Figure 6.1). Both sides of the skeleton are well represented, with elements from the right side being slightly more numerous (24 for the right side, against 19 for the left side, in MNE). The main elements missing are the small bones from both feet and both hands. The distal parts of the limbs are represented by only two metatarsals and one metacarpal. However, the identification of five hand or foot bones inside block UW88-B051 suggests that there might be at least one partially articulated foot/hand preserved inside.

### *1.1.2. MH2*

The overall percentage survival of MH2 is: 100 x 83/182 = 45.6% (Table 6.1; Figure 6.1). Except for the skull, all the major segments of the skeleton are present: mandible and teeth, forelimbs and hindlimbs, hands and feet, axial skeleton and pelvis. As for MH1, the right side of the skeleton is better represented than the left side (55 elements for the right side, 23 for the left). The distal limbs are well represented by the complete right hand, the partial left hand, the complete right ankle and one metatarsal.

## 1.2. Fragmentation

For both individuals, there are more partial bones than complete bones (59/42 for MH1 and 65/54 for MH2; Figure 6.2); however, the percentage of complete and near complete bones is still very significant (41.6% or almost half of the specimens for MH1 and 45.5% or almost half of the specimens for MH2; Figure 6.2).

The fragmentation ratios for MH1 and MH2 are:

- Fragmentation ratio for MH1 = NISP/MNE = 101/62 = 1.63
- Fragmentation ratio for MH2 = NISP/MNE = 128/83 = 1.54

Fragmentation ratios are slightly different, with MH1 showing a more significant degree of fragmentation than MH2 (Figure 6.2).

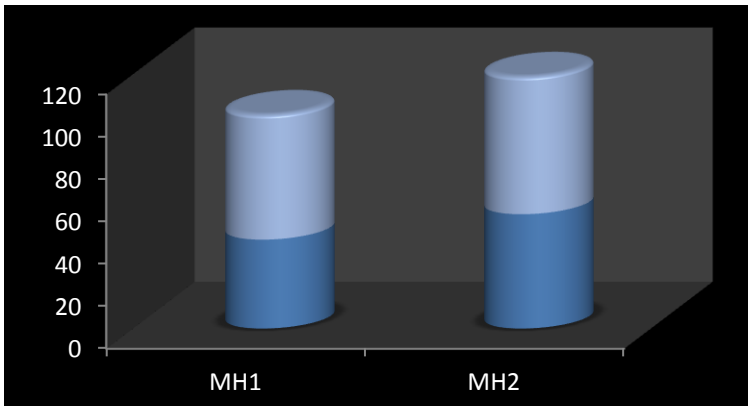



**Figure 6.2**. Percentages of complete (dark blue) and fragmentary bones (light blue) for MH1 and MH2.

### 1.3. Breakage pattern

*1.3.1. MH1*

The long bone edges for which an assessment of the breakage pattern was possible (*n.* 15) show breakage of weathered bones (*n.* 6) and the green fractures of fresh bone breaks (*n.* 8). Green fractures are observed on the edges of the four fragments of the right femur, while other long bones were already dry when the breakage took place.

*1.3.2. MH2*

An overwhelming majority (*n.* 17) of long bone edges for which a description of the breakage pattern was possible (*n.* 18) is characterised by fractures on weathered bones, while one green fracture, on a right femoral shaft fragment (UW88-53), was recorded.

## 2. DEGREE OF ARTICULATION

### 2.1. True articulations

MH1 does not have any elements still in articulation. Four anatomical parts of MH2 are still perfectly articulated (Figure 6.3; Table 6.2): the right ankle, composed of the distal tibia (UW88-97), the complete talus (UW88-98) and calcaneum (UW88-99); the right knee composed of the proximal tibia (UW88-78) and the right patella (UW88-79 and UW88-100); a part of the vertebral column composed of the two last thoracic vertebrae (UW88-43 and UW88-44); and the end of the vertebral column composed of the antepenultimate lumbar (UW88-127), the last lumbar vertebra (UW88-126 and UW88-138) and the sacrum (UW88-125 and UW88-137). In humans, the ankle, the lumbar vertebrae and the articulation sacrum/last lumbar vertebrae are all persistent articulations. The knee is an unstable or fragile articulation.

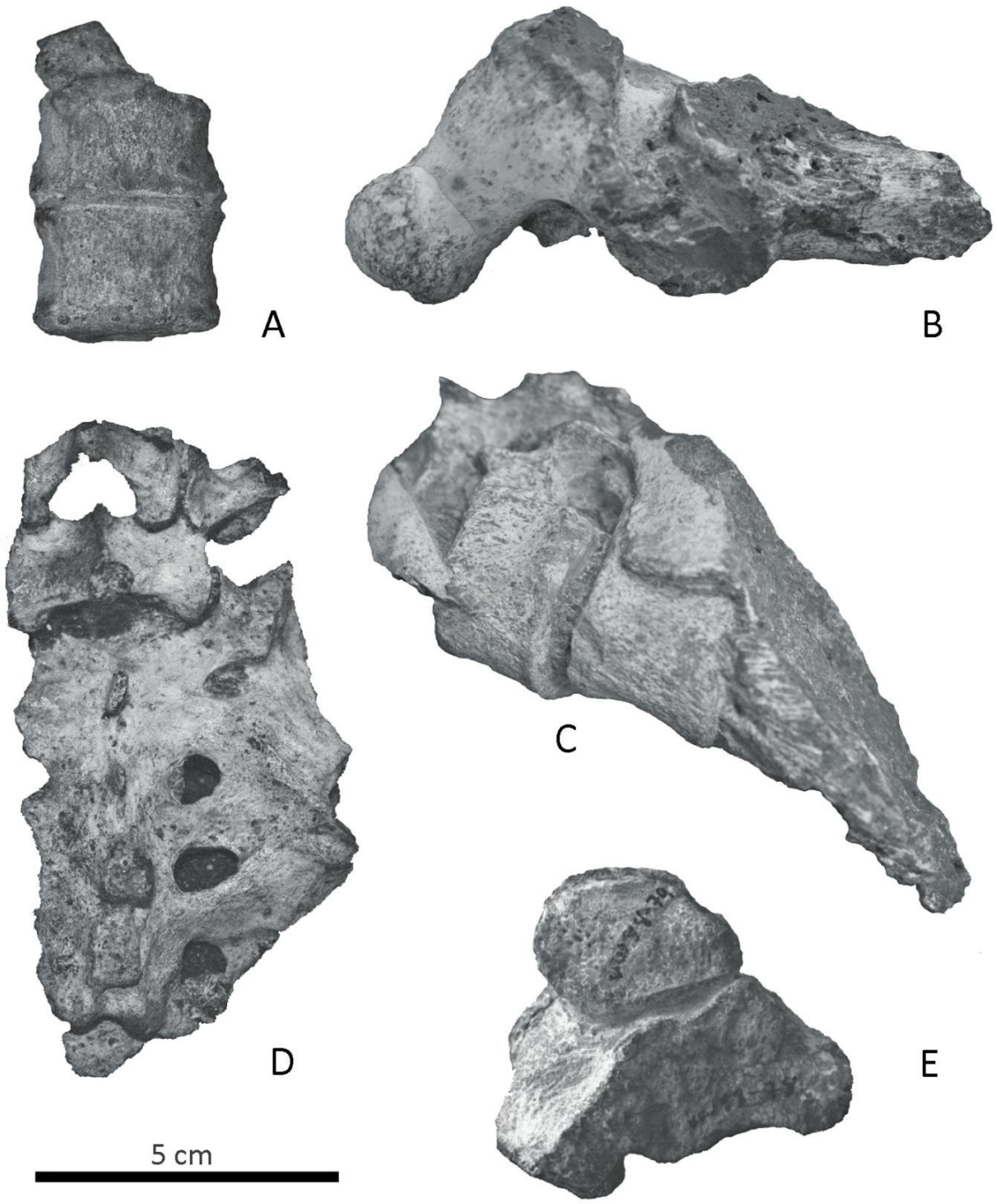



**Figure 6.3**. Hominin (MH2) articulations preserved. A: antepenultimate, last lumbar vertebrae and piece of the sacrum, B: right ankle, C: thoracic vertebrae, D: sacrum and last lumbar vertebrae, E: patella and proximal tibia.

## 2.2. Anatomical proximities

There are no bones in close anatomical proximity for MH1. For MH2, all the carpals, metacarpals and phalanges of the right hand are in close contact with each other, but not directly articulated (Table 6.2; Figure 6.4). Four thoracic vertebrae (UW88-188, 189, 190 and 191) from the "thoracic vertebrae block 2" (UW88-B742) are very close to each other, and in their anatomical position, but not in direct articulation (there is some sediment between them). Elements of the right side of the upper thoracic cage (first rib, clavicle and manubrium), the right scapula and humerus, and the right radius and ulna have undergone some minor displacement and are separated by a few centimetres of sediment, but the original anatomical position is generally respected. The same applies to the sacrum and the right pelvis that were found close to each other. All the preserved anatomical proximities of the MH2 skeleton (Table 6.2) correspond to unstable joints (hand, manubrium/clavicle) or interlocking unstable joints (scapula/humerus) in the human skeleton, except the sacrum/pelvis joint, which is a persistent articulation.

**Table 6.2**. Articulations preserved in MH2.

| Elements | Type of articulation | State of articulation |
|---|---|---|
| right hand (carpals, metacarpals, phalanges) | unstable | near articulation |
| manubrium and clavicle | unstable | anatomical proximity |
| sapula/humerus | interlocking unstable | anatomical proximity |
| Humerus/radius and ulna | unstable | anatomical proximity |
| four thoracic vertebrae | intermediate | anatomical proximity |
| sacrum and right pelvis | persistent | anatomical proximity |
| right ankle | persistent | articulated |
| right knee | unstable | articulated |
| two last thoracic vertebrae | intermediate | articulated |
| two last lumbar vertebrae | persistent | articulated |
| sacrum+last lumbar vertebra | persistent | articulated |
| elbow joint (humerus, radius and ulna) | unstable | disarticulated, close proximity |

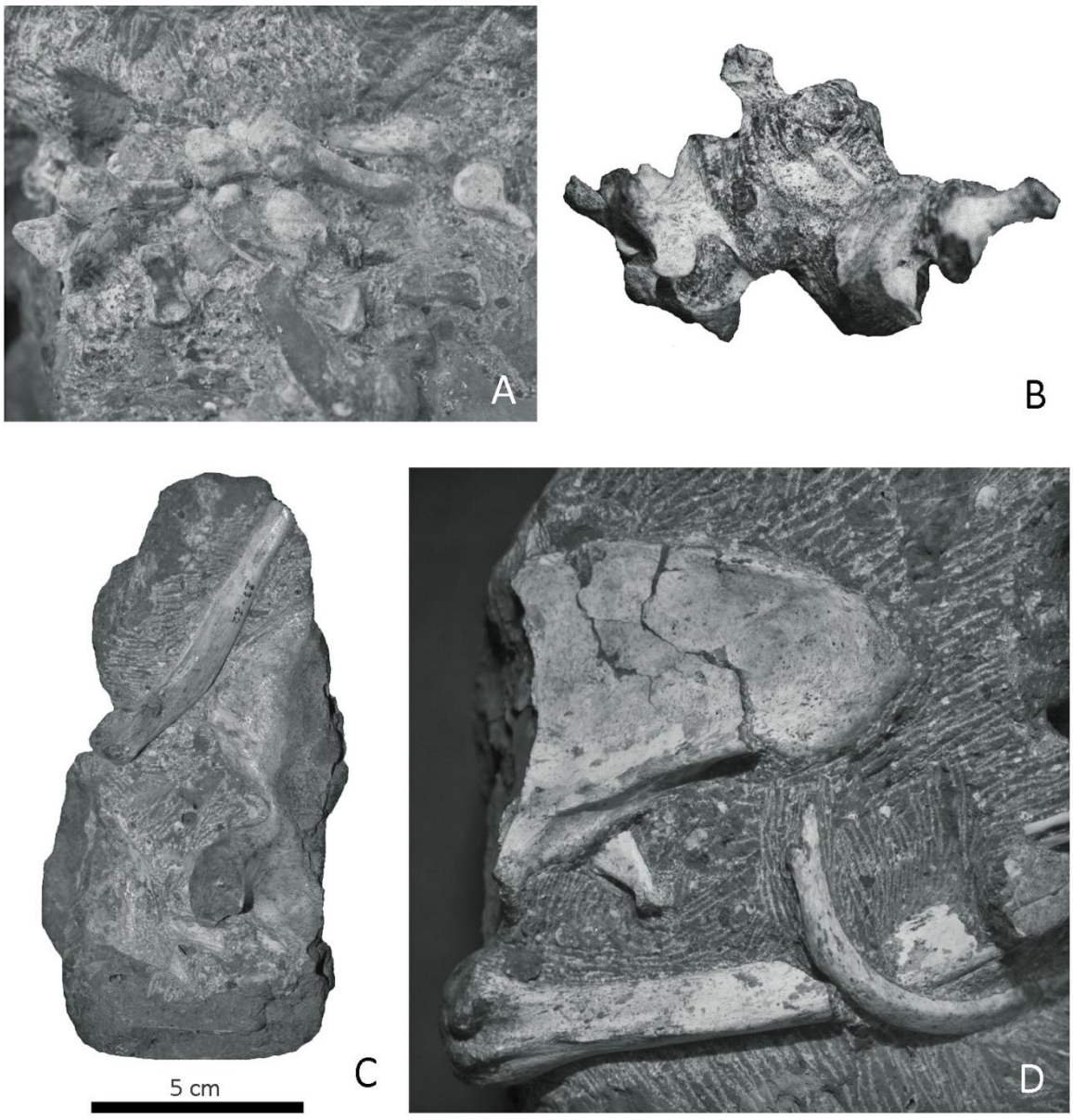



**Figure 6.4**. MH2 anatomical proximities. A: right hand bones, B: thoracic vertebrae, C: fragment of the right scapula associated with the right clavicle, and D: arm block containing the right scapula, right humerus and right first rib (below the scapula).

## 3. PRE- AND POST-DEPOSITIONAL DAMAGE

### 3.1. MH1 skeleton

*3.1.1. Modifications by abiotic agents*

Manganese precipitation

Manganese coating on bones can be an issue for the taphonomist as it obscures details of the surface, for instance cut marks, tooth marks, or insect damage. Manganese is frequently observed on fossils recovered from the dolomitic caves of the Cradle of Humankind (Cukrowska *et al*., 2005). The dolomite surrounding the breccias in which fossils are found is rich in manganese that is released when the dolomite dissolves and generally oxidizes to insoluble manganese dioxide. This results in the formation of small patches of microcrystalline manganese, which is precipitated in the contact between bone material and the surrounding matrix (Cukrowska *et al*., 2005). In order to assess how accurately a report on surface modifications reflects the true taphonomic history of a given assemblage, it is important to know how much of the material, and to what extent, is covered with manganese dioxide. When fossils are completely covered with manganese, fine modifications of the bone surface such as butchery marks, carnivore pits or insect damage, can be hidden by the manganese encrustation and invisible to the eye of the analyst, even when a microscope is used (Cukrowska *et al*., 2005).

As the majority of the MH1 bones were recovered from blocks of calcified sediment, the manganese coating is negligible. On 26.2% of the fossils the manganese is absent and 60.7% of the fossils display only small patches (category “slight”) (Table 6.3). Only one specimen exhibits significant manganese covering (category “moderate to heavy”). There is no specimen completely covered with manganese.

**Table. 6.3.** Manganese coating on MH1 bones.

| Category | absent | slight | moderate | moderate to heavy |
|---|---|---|---|---|
| No. of specimens | 16 | 37 | 7 | 1 |
| Percentage | 26.2% | 60.7% | 11.5% | 1.6% |

Bone weathering

All MH1 remains for which an estimation of the weathering stage was possible (*n.* 45) are weathered and exhibit superficial or moderately deep cracks, indicative of a period of subaerial exposure of the bones before burial. A little more than half of the specimens (*n.* 29) are slightly weathered (stage 1, with superficial cracks), while the remainder (*n.* 16) are more heavily weathered (stage 2, with deeper cracks and the beginning of surface flaking). No specimens show more extreme weathering (stages 3-5). The elements commonly displaying weathering stage 2 include right and left elements, from the upper and the lower body, and from both calcified and decalcified sediments (the innominate bone, the right clavicle, the right femur and humerus, three fragmentary ribs and the vault fragments).

Calcite crystal growth

Crystals of calcite are relatively common within MH1 bones; they occur in 28 specimens (45.9% of the total number of bones), inside either the medullary cavity of long bones, spongy parts or cracks on the surface of compact bones.

Red colour staining

36 bones (59% of MH1 remains) exhibit red traces. They consist of small dots and patches of a thin reddish layer, present on top of compact bones, including all types of skeletal elements, ribs, vertebrae, flat and long bones, skull and mandible. The origin of these red traces is the object of a study that will be published in the near future (Keeling *et al*., in prep.).

Sedimentary compaction

Seven specimens, including the right mandible and the skull, a fragmentary radial shaft, the distal part of the right femur, a fragment of the left ilium, a rib and a small fragment of scapula have been affected by compressive forces during sediment compaction, resulting in depressions, cracks and slight distortion of the bone surface.

Decalcification

There is no completely decalcified specimen, but 17 bones show the beginning of decalcification, with a small percentage of their surface presenting the white and chalky aspect consistent with the loss of calcium that was originally present in the bone. Most regions of the skeleton (long bones, metapodials, skull, vertebrae, and ribs) present decalcification.

*3.1.2. Modifications by biotic agents*

Trampling

No definitive trample mark has been recorded on the MH1 fossils.

Root growth

Recent and modern damage caused by the action of roots and rootlets is only observed on the right clavicle of MH1 (specimen UW88-1). It is most certainly consistent with recent vegetal damage, as the clavicle was exposed on the surface of the block of calcified sediment from which it was recovered.

Carnivore, bird of prey, rodent and anthropogenic damage

There is no evidence of carnivore, rodent, bird of prey or anthropogenic damage on any of the MH1 remains. No chewed, digested or burnt bone was recorded and no tooth, butchery, beak or talon mark was observed.

Invertebrate damage

Four remains of MH1 exhibit invertebrate damage, namely the upper right incisor and canine (UW88-29 and UW88-30), the left ischium and ilium (UW88-14 and UW88-102). The teeth were recovered during sieving of *in situ* decalcified sediments, while the other elements come from *ex situ* calcified sediment. The modifications consist of intersecting striations, pits and surface gnawing (Figures 6.7 and 6.8). Some of the features closely resemble the damage produced by hide beetles during experimental study but the exact identity of the species at the origin of the modifications is still investigated (Backwell *et al*., in prep.).

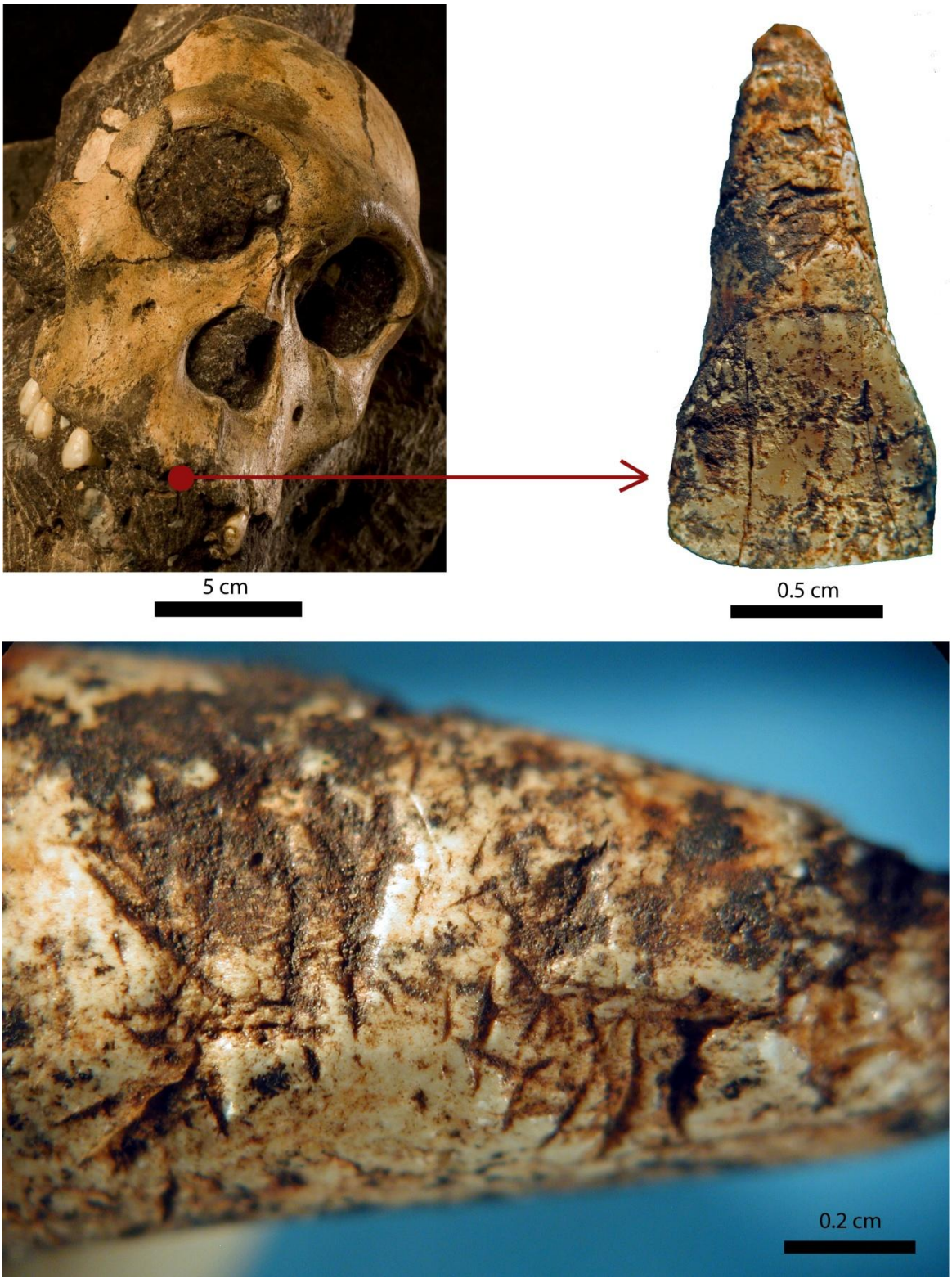



**Figure 6.5.** Invertebrate modifications on MH1 upper right incisor (specimen UW88-29).

On the teeth, the traces are located on the tooth roots, below the manganese coating (Figure 6.5), implying that they were produced after the teeth had fallen out of their sockets and detached from the skull, but before decalcification of the sediment and manganese precipitation. On the pelvis fragments they are located on the periosteum, either below (ilium) and on top (ischium) of the manganese coating (Figure 6.6), possibly indicating two waves of insect action on the bones, taking place at two different times.

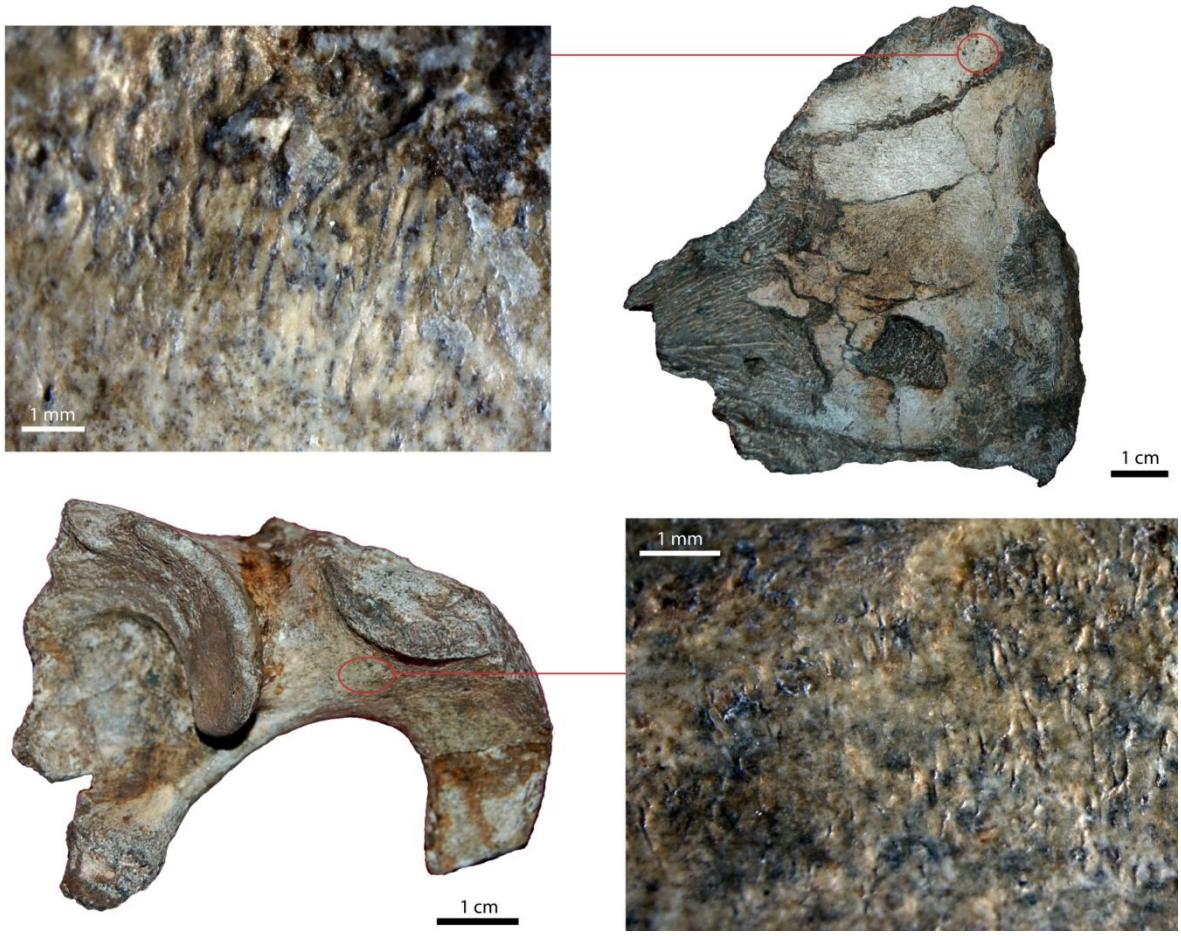



**Figure 6.6.** Invertebrate modifications on MH1 left ilium (specimen UW88-102) and left ischium (specimen UW88-14).

## 3.2. MH2 skeleton

### *3.2.1. Modifications by abiotic agents*

Manganese precipitation

The manganese coating is negligible on MH2 remains (Table 6.4). Most of them present either no manganese or only small patches covering less than half the bone surface (categories “slight” and “slight to moderate”). Six bones have manganese on half of their surface (category “moderate”). There is no specimen with significant coating (categories “moderate to heavy” and “heavy”) (Table 6.4).

**Table 6.4**. Manganese coating on MH2 bones.

| Category | absent | slight | slight to moderate | moderate |
|---|---|---|---|---|
| No. of specimens | 36 | 54 | 9 | 6 |
| Percentage | 34.3% | 51.4% | 8.6% | 5.7% |

As for MH1, the limited impact of manganese coating on MH2 fossils permits the identification of microscopic modifications of the bone surface, if any, as they would not be masked by a deposit of manganese.

Bone weathering

All MH2 bones for which an estimation of the weathering stage was possible (*n.* 70) exhibit superficial or moderately deep cracks, indicative of a period of exposure of the bones before burial. The majority of the specimens (*n.* 59) are slightly weathered (stage 1, with superficial cracks), while the rest (*n.* 11) are more weathered (stage 2, with deeper cracks and beginning of surface flaking). There is no specimen showing extreme weathering (stages 3-5). The elements characterised by weathering stage 2 include bones from the right and the left side, only from the upper body, and only from calcified sediment (fragments of the right and left hemi-mandibles, six ribs, and the pollical proximal right phalanx).

Calcite crystal growth

Calcite crystals are present on 77 specimens (73.3%), inside the medullar cavity of long bones, inside spongy bones or in cracks on top of compact bones.

Red colour staining

Thin patches or dots of reddish colour are observed on 18 specimens (17.4%), including long bones (the right femur, humerus and tibia), tarsals (the right talus and calcaneum), a fragment of the innominate, the sacrum, the left mandible and various ribs.

Sedimentary compaction

Eleven specimens (10.5%), including ribs, the right scapula, humerus and ulna, the left clavicle, the right distal tibia and the right ilium, have been affected by sedimentary compression, resulting in impacts, cracks and slight distortion of the original bone surface.

Decalcification

44 bones (41.9%) show the beginning of decalcification, with only a small percentage of the bone surface presenting the white chalky aspect due to the loss of calcium initially present in the bone. The process of decalcification affects almost all types of skeletal elements, namely long bones, flat bones, metapodials, carpals and tarsals, ribs and vertebrae.

*3.2.2. Modifications by biotic agents*

Trampling

None of the MH2 bones presents any definitive trample mark.

Root growth

There is no damage associated with the action of roots or rootlets on MH2.

Carnivore damage

*Observations on the fossils*

The first right rib of MH2 (specimen UW88-198) exhibits two pits evoking possible chewing damage caused by a mammalian carnivore (Figure 6.7). The rib is currently embedded in calcified sediment, below the scapula. It is therefore only possible to examine the pits on the 3D rendering of the bone, produced from micro-CT scanning data (Figure 6.7). There is one pit on the cranial side of the rib and one on the caudal side. The dimensions of the pits (Table 6.5) have been obtained from the 3D rendering, using the Avizo 6.3 software. They are consistent in size with pits produced by large carnivores (e.g. spotted hyaenas, lions) (Selvaggio and Wilder, 2001; Domínguez-Rodrigo and Piqueras, 2003; Table 6.5).

**Table 6.5.** Dimensions (respectively: mean and range) of the possible tooth pits observed on MH2 right first rib (in mm), and dimensions of tooth pits experimentally produced by different class-sized carnivores (data from Selvaggio and Wilder, 2001, and Domínguez-Rodrigo and Piqueras, 2003).

| Pits | Length | Breadth |
|---|---|---|
| MH2 first rib | 4.00 [3.5-4.5] | 2.30 [1.7-2.9] |
| Spotted hyaenas | 3.27 [1-5.5] | 2.24 [0.9-3.5] |
| Lions | 3.45 [3-4] | 2.20 [1.8-2.5] |
| Leopards | 2.00 [1.5-2.5] | 1.00 [0.2-1.8] |
| Cheetahs | 1.75 [1.5-2] | 1.00 [0.8-1.2] |
| Jackals | 1.45 [0.5-2] | 0.85 [0.3-1.2] |

*Definitive attribution of the pits to carnivore damage: discussion*

The attribution of the two pits described above to chewing modification caused by a large carnivore is subject to discussion. Several arguments are considered here that dismiss the definitive attribution of the pits to carnivore damage. Firstly, the pits constitute a very isolated evidence of carnivore action in the hominin assemblage, and are not confirmed by any other evidence of carnivore activity (no other chewing damage recorded on the hominin remains, no digested bone in the assemblage, no fresh breakage associated with carnivore tooth marks, no selective body part representation associated with carnivores). The presence of carnivore tooth pits on the MH2 specimen is not

consistent with the general state of preservation of that individual, which is characterised by complete bones, almost all skeletal parts preserved, and elements still in articulation. The first rib was recovered in an anatomically predictable position (i.e. close to the manubrium, the right clavicle and scapula), which indicates it has not suffered any major displacement. Furthermore, a large carnivore would most likely have destroyed the rib, which is a fragile and thin bone.

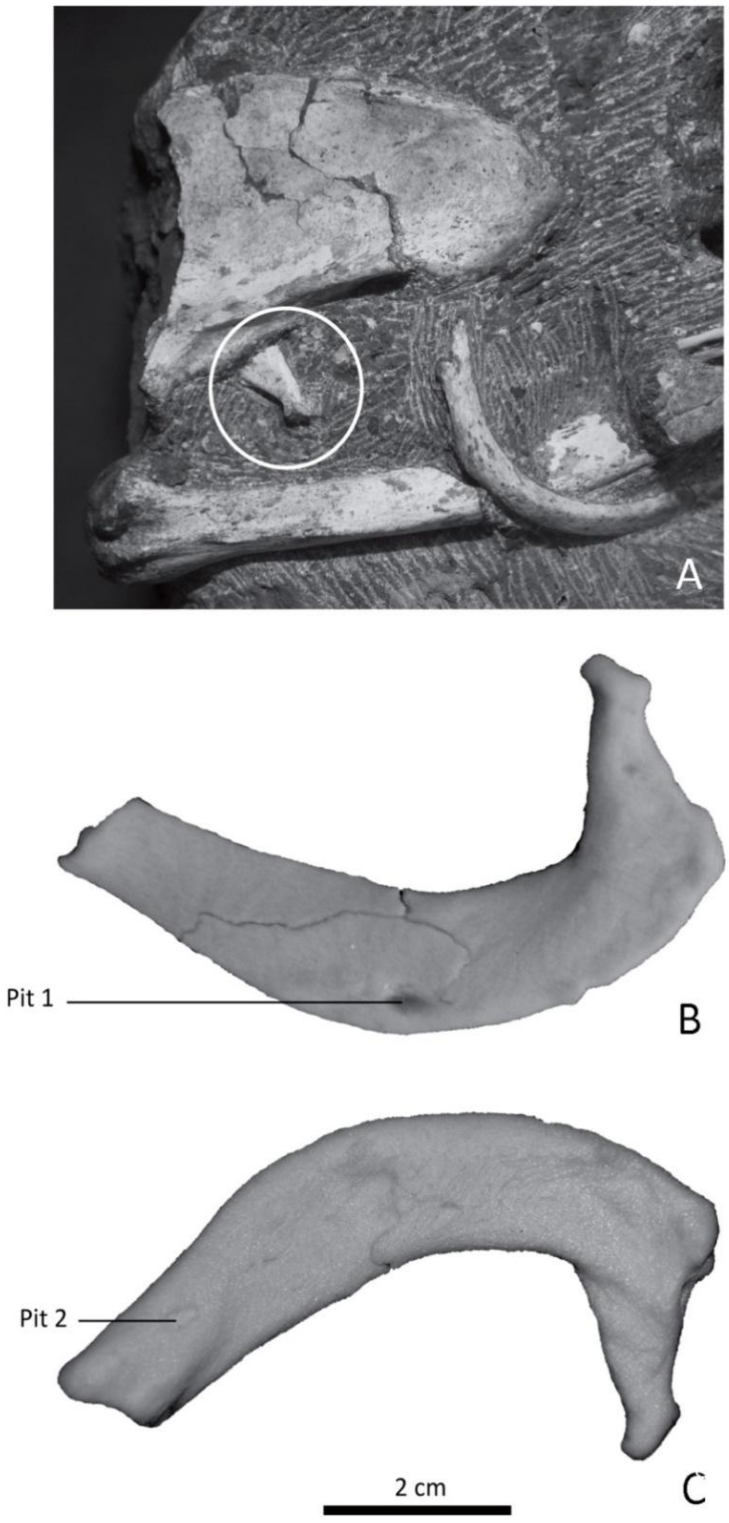



**Figure 6.7.** MH2 first right rib showing possible carnivore tooth pits. A: provenance of the rib, below the scapula in the "arm block"; B and C: pits 1 and 2 observed on the caudal (B) and cranial (C) surfaces of the rib and illustrated here on the printout.

The pits observed on the rib are associated with cracks on the bone surface (Figure 6.6) and their morphology is consistent with indentations caused by falling rocks. Consequently, carnivore chewing is regarded as a very unlikely explanation.

Bird of prey, rodent and anthropogenic damage

On MH2 skeleton, there is no indication of any type of damage inflicted by a rodent or a bird of prey (no chewed or digested bone, no beak or talon impact). There is also no evidence for modifications produced by hominins, in the form of butchery marks, percussion impacts or burnt bones.

Invertebrate damage

A fibula shaft fragment (UW88-84), recovered from *ex situ* sediment, shows invertebrate damage. The modifications consist of intersecting striations and surface gnawing, located below the manganese, which imply they are most certainly pre-burial, or at least ancient (Figure 6.8). They are similar to the insect marks observed on MH1 fossils.

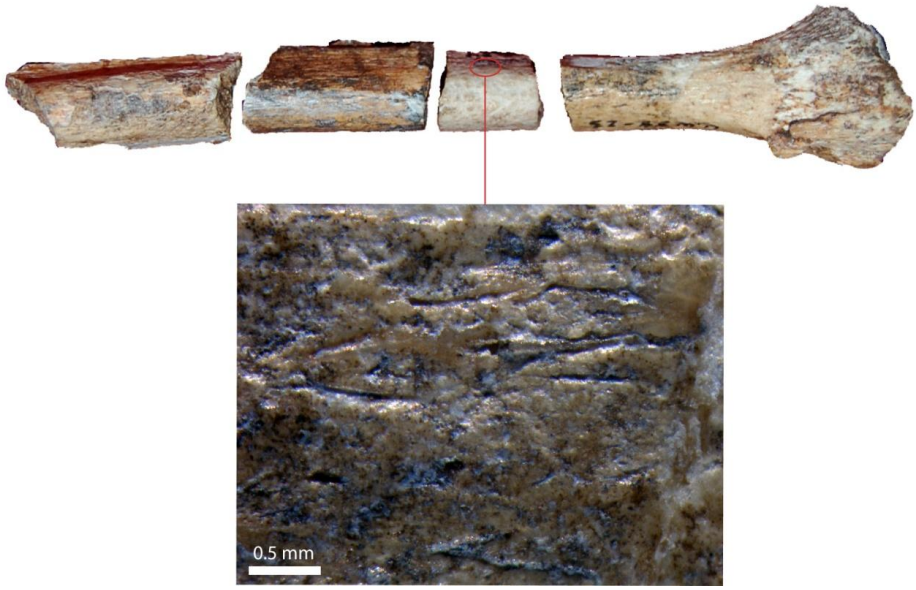



**Figure 6.8.** Invertebrate modification observed on a fibula shaft fragment (specimen UW88-84) belonging to MH2.

## 4. COMPARISON BETWEEN THE TWO INDIVIDUALS IN TERMS OF PRESERVATION

### 4.1. General preservation

#### *4.1.1. Similarities*

MH1 and MH2 present an excellent degree of preservation, in terms of percentage survival of body parts, abundance of complete and near complete bones, and presence of articulated and near-articulated elements for MH2. For both individuals, the skeletal part representation is not consistent with a density-mediated pattern, where the denser parts are more abundant than the fragile bones. Very fragile elements such as the blade of the scapula are preserved (i.e. complete right scapula of MH2) and very spongy bones are also well-represented (the vertebrae for instance have a percentage survival of 48% for MH1 and 44% for MH2). Based on the high level of completeness and the fact that all anatomical sections and elements from both sides are present for the two individuals, I argue that the skeletons were complete and probably alive when they arrived in the cave deposit. Consequently, the missing elements are either still *in situ* in the deposit at the site, or in the laboratory, in blocks of matrix that have not yet been prepared.

#### *4.1.2. Differences*

The major difference in terms of general preservation concerns the degree of articulation of recovered remains. While articulated and near articulated skeletal elements have been preserved for MH2, there is none for MH1. The difference in preservation may be explained by a difference in age between the two individuals or more likely a difference in the length of *post-mortem* pre-burial exposure.

Another notable difference concerns the number of recovered remains, which is higher for MH2 than for MH1. However, as proved by the recent identification of new fossils belonging to MH1 in a block of calcified sediment, it seems that this difference is purely due to recovery bias. The lesser degree of articulation for MH1 implies a potential

for higher dispersal inside the deposits, and consequently a smaller number of MH1 elements than MH2 that have been recovered. It is highly likely that all of the remains of MH1 and MH2 will eventually be found (see above), rendering the difference in MNE between the two individuals negligible.

### 4.2. Bone surface damage

MH1 and MH2 present a generally very similar state of preservation of their bones and bone surfaces. The pre- and post-depositional agents that have affected their bones are the same. The differences noticed between the two individuals concern the intensity of the damage rather than the nature of it (Figure 6.9).

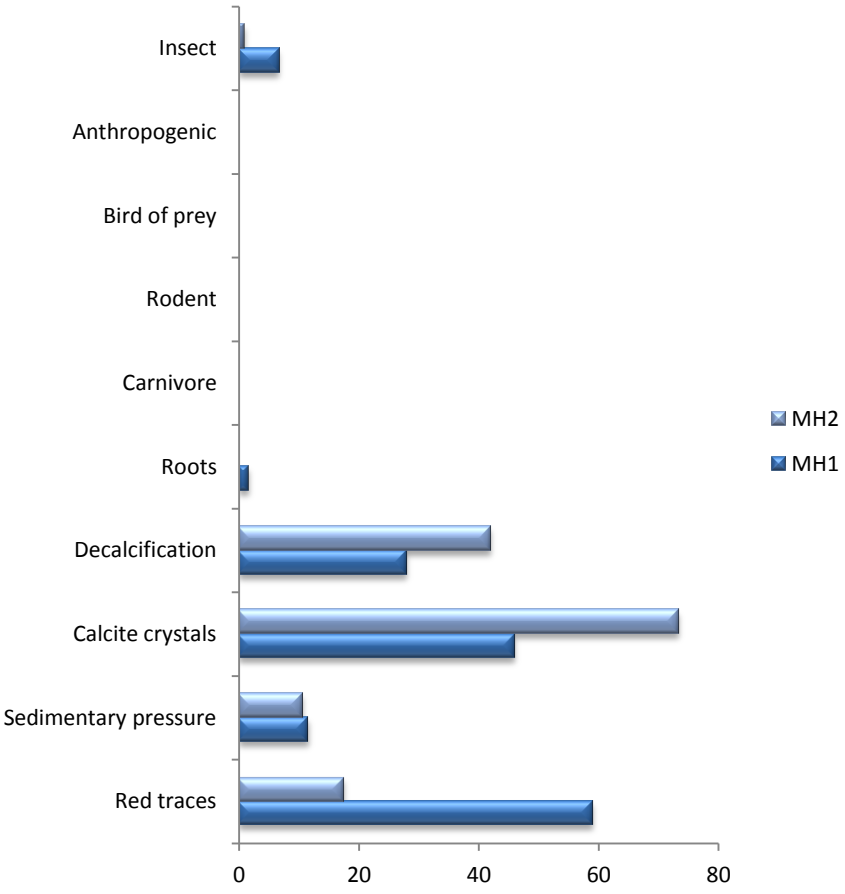



**Figure 6.9.** Modifications of the surface of MH1 and MH2 fossils, caused by biotic and abiotic agents (the data are presented as a percentage of remains affected by each type of modification).

*4.2.1. Similarities*

Numerous similarities between MH1 and MH2 can be highlighted. The degree of manganese coating (Tables 6.3 and 6.4), the intensity of sedimentary pressure, the root damage, as well as the absence of anthropogenic, rodent, bird of prey, and carnivore-induced modifications are the same for the two individuals.

Pre-burial processes: near-absence of biotic damage

Modifications caused by biotic agents, which are absent from both individuals, with the exception of invertebrate damage, are consistent with peri- and post-mortem but pre-burial processes. The absence of such modifications indicates that avian or mammalian carnivores whether hunters or scavengers, and rodents, played no role in the death of the hominins and had no access to the carcasses when decomposition took place. On that matter, MH1 and MH2 seem to share a similar scenario. The absence of trample marks for both MH1 and MH2 confirms the absence of physical disturbance of the corpses as the bones were becoming exposed. This can either mean that the bodies were buried before their bones were exposed, or that animals, including hominins, had no access to the carcass during decomposition and could not have trampled them.

Post-depositional processes: manganese and sedimentary pressure

Manganese dioxide encrustation of the bones and sedimentary pressure causing compaction are post-durial processes. The deposition of manganese on bones usually takes place during decalcification of the breccia (Cukrowska *et al*., 2005), possibly relatively recently in terms of the taphonomic history of the hominins. The impact of sediment compaction on the fossils occurs after burial of the skeletons by sediment and collapsed blocks from the roof deeply enough to actually cause the bones to collapse (Brain, 1981). The similarities observed between MH1 and MH2 in terms of intensity of manganese coating and sediment compaction can be explained by the close proximity in which MH1 and MH2 were recovered inside the deposit. They are likely to have

undergone the same pressure from the sediments above them and the same process of manganese deposition.

### *4.2.2. Differences*

Pre-burial processes: weathering and invertebrate damage

MH1 is generally more weathered than MH2, with a higher percentage of specimens having reached weathering stage 2 than for the female (Table 6.6; Figure 6.10).

**Table 6.6.** Weathering stages of MH1 and MH2 remains (in percentage).

| Weathering | MH1 | MH2 |
|---|---|---|
| Stage 1 | 39% | 47.1% |
| Stage 2 | 32.8% | 11.8% |

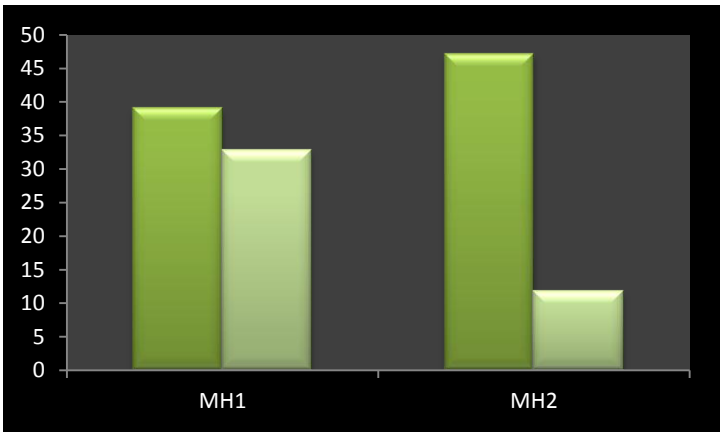



**Figure 6.10.** Comparison of MH1 and MH2 specimens according to the weathering stages (dark green: stage 1; light green: stage 2, following Behrensmeyer, 1978).

The implications of this difference will be discussed in further detail in Chapter 8. The variability between MH1 and MH2 in terms of weathering could be explained by temporal and micro-environmental factors, such as a difference in the time of subaerial exposure, a difference in the time of entry inside the cave, and a difference in the rate of burial. It could also be linked to a slight difference in process of decomposition inside the cave, associated with different conditions of temperature and humidity.

With regard to invertebrate damage, more specimens of MH1 are affected than MH2 (four remains for MH1 contra only one for MH2). Because the female preserves more remains than MH1 (MNE: 119 for MH2 contra MNE: 64 for MH1), one would expect to observe more insect damage on her bones. However, the difference is too small and applies to a sample too limited in size to be statistically significant. Furthermore, not all invertebrates actively select bones for consumption, so marks left by them, whether during feeding or pupating on the carcass, are accidental. It follows that the abundance of marks on the bones does not necessarily correlate with the intensity of insect action on the skeleton.

Post-depositional processes: red traces, decalcification and crystals of calcite

Percentages of remains showing red traces, the beginning of decalcification, and crystals of calcite vary between MH1 and MH2. There is a higher percentage of remains with calcite crystals and decalcification for MH2 than for MH1, while there is a higher percentage of remains with red traces for MH1 than for MH2 (Figure 6.9).

The origin of red traces is currently under study (Keeling *et al*., in prep.), so will not be discussed further here. Explaining the difference observed between the two individuals in terms of abundance of these marks remains difficult.

The decalcification of the bones and the formation of calcite crystals inside them are directly linked to chemical processes affecting the breccia in which the fossils are preserved and the surrounding dolomite. These chemical processes (dissolution of the dolomite, decalcification of the breccia, precipitation of calcite) can be extremely variable inside the same deposit and depend upon numerous factors (e.g. climatic and environmental conditions outside and inside the cave; microbial activity inside the cave; depth and degree of opening of the cave; see for example Brain, 1981; Jones, 2001; Chalmin *et al*., 2007). For instance, infiltration of water can cause localised dissolution of a pocket of breccia, leading to the decalcification of the bones it contains, while the

surrounding sediment will remain calcified. A difference in terms of percentage of bones affected by decalcification and crystals of calcite inform about chemical micro-variations inside the deposit, but do not reflect major differences between MH1 and MH2 in terms of post-depositional taphonomic history.

# Chapter 7. Reconstruction of the burial posture of the hominins

This chapter presents the results of the spatial approach and proposes a reconstruction of the original burial position of MH1 and MH2 inside the deposit. It includes firstly a description of the origin of the hominin fossils, whether from *in situ* calcified or decalcified sediment, or *ex situ* blocks removed during mining, together with their exact position and orientation, when known. Secondly, the results of the analysis of movement, direction and transportation of the hominin fossils inside the deposit are offered and discussed. This section also considers geological information regarding the stratigraphy and the general orientation of the sediments of Facies D, which contains the hominins. Finally, hypotheses regarding 3D refitting in the deposit of *ex situ* hominin fossils are proposed. Combined with a virtual reconstruction of the cave, this information permits a visualization of the position in which the hominins where buried, prior to mining of the deposit.

## 1. STRATIGRAPHIC ORIGIN OF THE HOMININ REMAINS

The following section provides a more detailed description of the MH1 and MH2 hominin remains, together with their exact stratigraphic provenance. Two categories are considered: (1) the remains found *in situ* and which were assigned coordinates, and (2) those found *ex situ* in blocks removed by the miners (for a complete list of the hominin specimens with their provenance, see Appendix 1; for the coordinates of the *in situ* hominin remains, see Appendix 2).

### 1.1. MH1 *in situ* remains

Two fragments of the right cranial vault (UW88-31, the right parietal and UW88-32, a fragment of the right temporal) were recovered *in situ* at the very bottom of Facies D, just above Facies D (Figure 7.1). They are part of the MH1 skull, which now lacks only the right part of the calvaria. The right upper first incisor (UW88-29) and canine (UW88-30) were found during water sieving of *in situ* sediment for which 3D coordinates were recorded.

Two right near-complete metatarsals (UW88-16 and UW88-22) were found *in situ* in the western part of Facies D (Figure 7.1) and assigned to MH1.

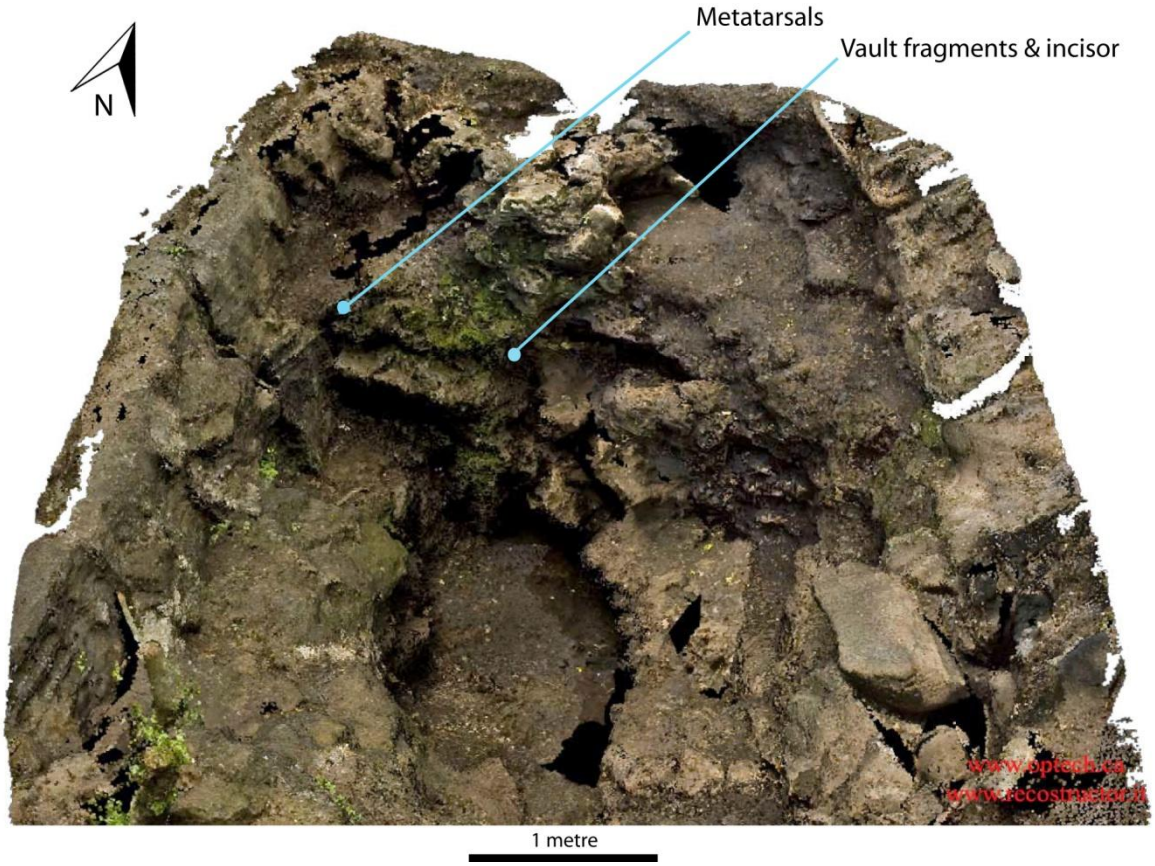



**Figure 7.1.** Position of the *in situ* MH1 remains in Facies D and E (image: courtesy of D. Conforti, Optech Company, modified).

## 1.2. MH1 *ex situ* remains

### *1.2.1. "Clavicle block"*

The first breccia block recovered from the site was found 15 m from the main pit and contained an exposed clavicle (UW88-1; Figure 7.2). This block, now referred to as the "clavicle block" (Figures 7.2 and 7.3), has exposed on its surface a fragment of the left hemi-mandible preserving the lower canine (UW88-2) (Figure 7.2). The right hemi-mandible (UW88-8) was found in the same block during preparation. The block also contains an ulna (UW88-3), several fragments of the pelvic bone (UW88-6, the anterior

portion of the right ilium; UW88-7, the posterior portion of the right ilium; UW88-14, the near complete left ischium), a complete cervical vertebra (UW88-9), a near complete thoracic vertebra (UW88-11), a right radius (UW88-12), a distal right rib fragment (UW88-13), a proximal left rib fragment (UW88-15), a fragment of a rib shaft, side indeterminate (UW88-17) and a fragment of the right acromion process (UW88-113).

**Figure 7.2.** "Clavicle block" on the day of discovery showing the right clavicle UW88-1 on one side (left) and a fragment of the right mandible UW88-2 (right) on the other (image: courtesy of L.R. Berger).


**Figure 7.3**. Partially prepared upper part of the "clavicle block" showing the mandible (UW88-8) next to the ulna (UW88-3) and the cervical vertebra (UW88-9).

### *1.2.2. Right femur*

The proximal right femur (UW88-4) was found at the site in an *ex situ* block (Figure 7.4). Together with three other loose fragments (UW88-5, a proximal shaft fragment; UW88-39, part of the proximal head; and UW88-89, a medial shaft fragment) it constitutes the near-complete right femur.

**Figure 7.4.** Lee Berger at Malapa holding the block containing the proximal femur UW88-4 and a modern femur for comparison (image: courtesy of L.R. Berger).

### 1.2.3. "Skull block"

The "skull block" was found *ex situ*. It contains the complete right humeral shaft (UW88-42), the proximal head of the left humerus (UW88-36) and the near-complete skull (UW88-50) (Figure 7.5).

**Figure 7.5.** Superior view of the "skull block" showing the partially prepared skull (UW88-50) and the right humeral shaft (UW88-42). Scale bar = 10 cm.

### 1.2.4. “Ilium block”

The “ilium block” contains the right distal humerus (UW88-88) and the left ilium (UW88-102) (Figure 7.6). The distal humerus fits perfectly with the humeral shaft present in the “skull block”. The breakage is due to mining.

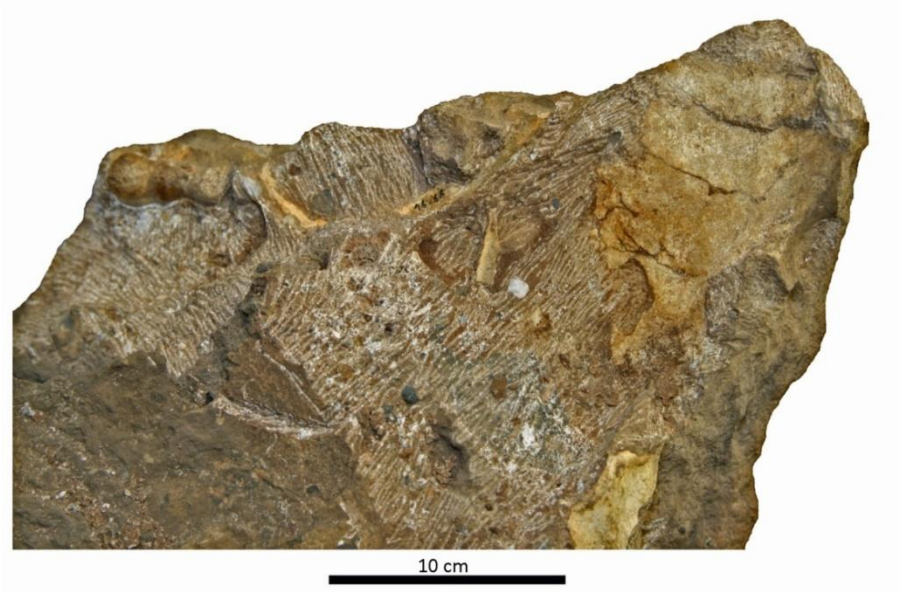



**Figure 7.6.** View of the “ilium block” showing the distal right humerus (UW88-88) on the left and the left ilium (UW88-102) on the right.

### *1.2.5. Block UW88-B051*

A block (UW88-B051) of calcified sediment recovered *ex situ* and containing on its surface an articulated humerus and ulna of a bovid was CT-scanned at the Charlotte Maxeke hospital. It has not been physically prepared yet and the virtual preparation is in progress. Observations of the scanning data have revealed the presence inside the block of numerous bones that are attributed to MH1 (Figures 7.7 and 7.8).

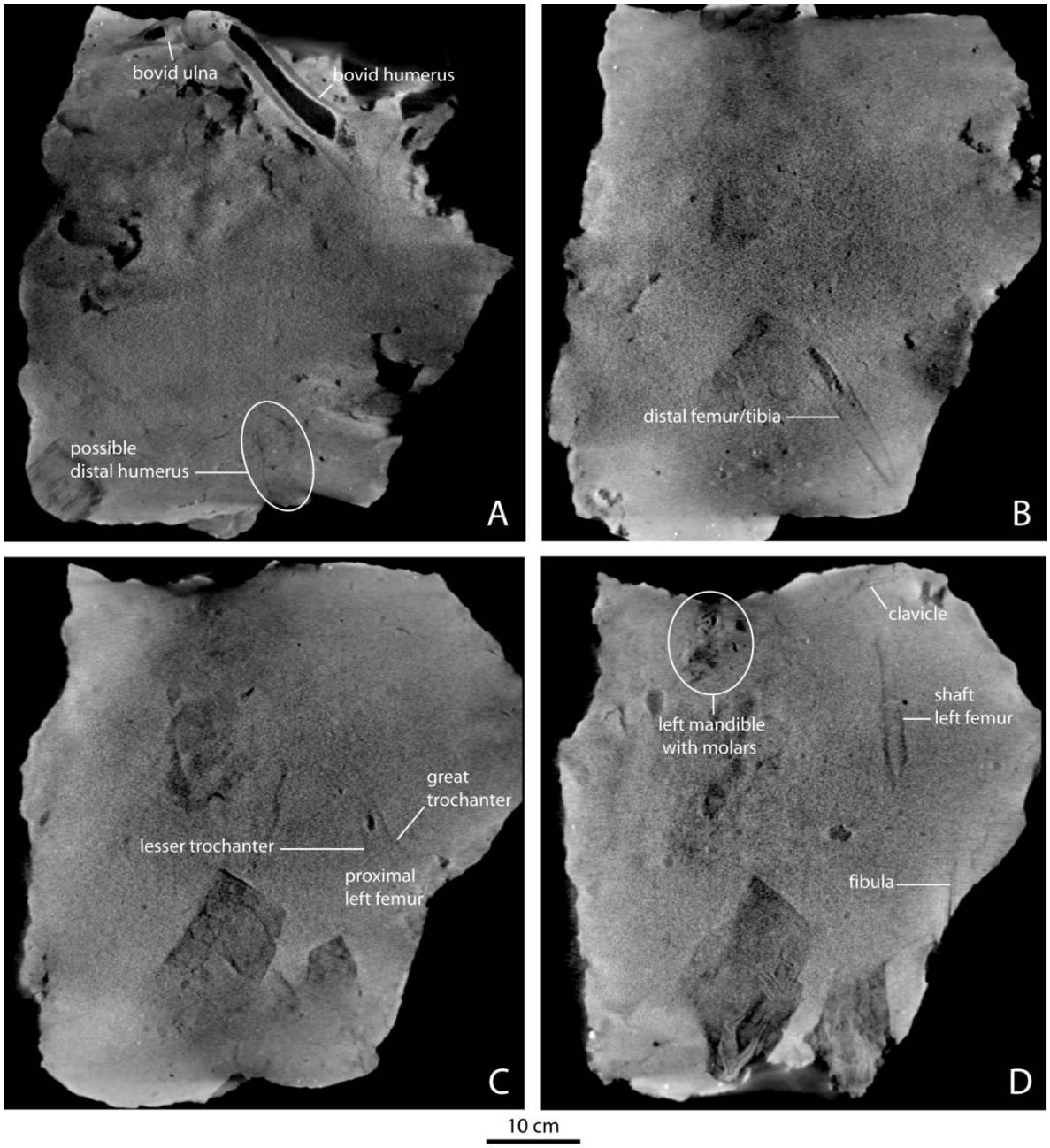



**Figure 7.7**. Bones preserved inside the block of calcified sediment UW88-B051 attributed to MH1, from the top (A) to the middle of the block (D), shown as snapshots of the CT-scanner data realized with Avizo.

The block contains the left clavicle, femur and mandible, the distal right ulna, at least four ribs, five hand or foot bones, a fibula, two possible fragments of humerus (a shaft and a distal fragment), and a possible tibia or distal femur (Figures 7.7 and 7.8).The distal right ulna from this block refits with the proximal right ulna from the "clavicle

block", while the left mandible refits with the left fragment of mandible bearing the lower canine, also from the "clavicle block". This means that a direct refitting between the "clavicle block" and the block B051 is possible.

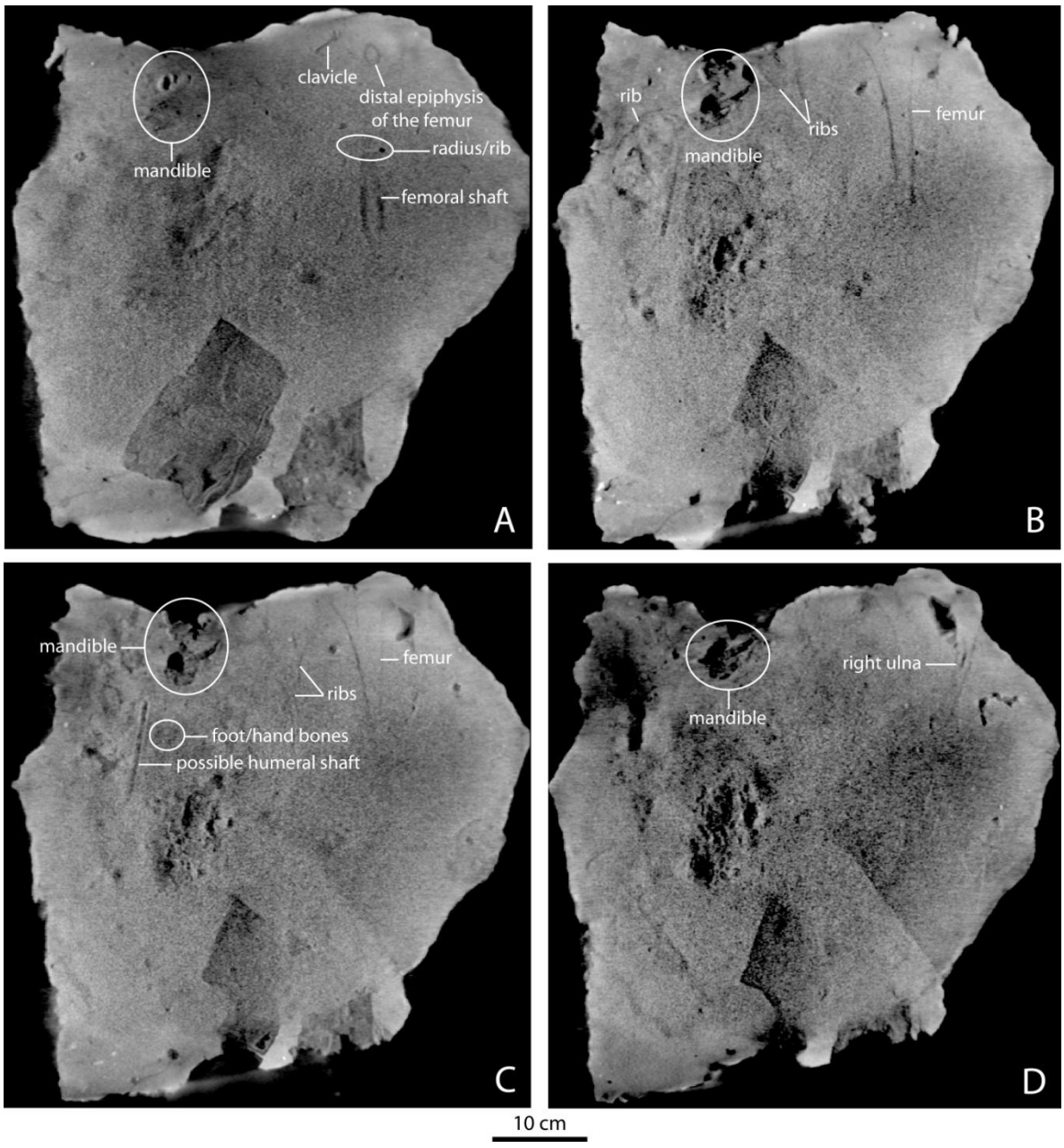



**Figure 7.8**. Bones preserved inside the block of calcified sediment UW88-B051 attributed to MH1, from the middle (A) to the lower part of the block (D), shown as snapshots of the CT-scanner data realized with Avizo.

### *1.2.6. Other remains*

The first lumbar vertebra (UW88-152) and the intermediate shaft of a rib (UW88-155) were found together in the same *ex situ* block (UW88-B245). Two intermediate right ribs (UW88-41 and UW88-86) were found together in the same *ex situ* block. The other specimens were found in various *ex situ* blocks, during preparation. A list of those remains is given below:

- Parts of the pelvic bone**:** two iliac fragments, side indeterminate (UW88-67 and UW88-206), and one pelvic fragment, side indeterminate (UW88-27).

- Fragments of scapula (UW88-35, a possible scapula fragment; UW88-68, a scapula fragment, and a left scapula fragment, UW88-197, from block UW88-B057) come from *ex situ* blocks and do not refit with one another.

- A right metacarpal (UW88-112).

- Long bones: a right humeral head (UW88-34), a left distal ulna (UW88-130), some radial shaft fragments (side indeterminate: UW88-18 and UW88-75) and two long bone shaft fragments, side indeterminate (UW88-26 and UW88-77).

- Ribs: the first right rib (UW88-148); one distal rib fragment, side indeterminate (UW88-74); one fragment of a central rib shaft, side indeterminate (UW88-211); a possible right rib fragment (UW88-141) and a fragment from the sternal end of a rib, side indeterminate (UW88-76).

- Vertebrae: a fragment of a cervical vertebra (UW88-71), a complete lumbar vertebra (UW88-92), four near complete thoracic vertebrae (UW88-37, UW88-69, UW88-70, UW88-90), two cervical vertebrae (UW88-72 and UW88-93) and an unidentified vertebra (UW88-73).

## 1.3. MH2 *in situ* remains

The “arm block” (UW88-B043) contains most of the remains that belong to the adult individual (Figures 7.9 and 7.10). It was found *in situ* in Facies D (Figure 7.9).


**Figure 7.9.** Position of the MH2 “arm block” *in situ* in Facies D (image: courtesy of D. Conforti, Optech Company, modified).

It contains the complete right humerus (UW88-57), the complete right radius (UW88-85), the complete right ulna (UW88-62), the near-complete right scapula (UW88-28), the right distal femur broken into two pieces (UW88-63 and UW88-53), five right carpals (capitate, UW88-156; scaphoid, UW88-158; lunate, UW88-159; triquetral, UW88-163; hamate, UW88-95), five complete metacarpals (first, UW88-119; second, UW88-115; third, UW88-116; fourth, UW88-117; fifth, UW88-118), five complete right proximal manual phalanges (thumb, UW88-160; second, UW88-164, third, UW88-120; fourth, UW88-108; fifth, UW88-121), four complete intermediate right manual phalanges

(second, UW88-123; third, UW88-161, fourth, UW88-122; fifth, UW88-162), the right pollical distal phalanx (UW88-124), a complete right intermediate rib (UW88-61), the near-complete right second rib (UW88-58), the third right rib (UW88-166), some right rib fragments (UW88-59, UW88-60, UW88-143, UW88-144, UW88-145, UW88-165, UW88-175), a vertebral fragment (UW88-66) and the sternal end of the right clavicle (upper part of the arm block, UW88-142) (Figure 7.10). The manubrium (UW88-172), together with a near complete intermediate rib (UW88-154) and the near-complete right first rib (UW88-198), are located just below the scapula (Figure 7.11).


**Figure 7.10.** Superior view of the "arm block" (UW88-B043) showing the right scapula, first and second ribs, humerus, and distal radius and ulna.

The right knee was found on top of the arm block and broke during the removal of this block. It was located on the north-western corner of the arm block, near the distal

femur (UW88-63). It is partly preserved and consists of a fragment of the proximal right tibia epiphysis (UW88-64), which fits directly with another proximal right tibia epiphysis fragment (UW88-78), the latter of which is in articulation with the right patella (UW88-79 and UW88-100). The breakage of the patella into two pieces happened during the excavation process.

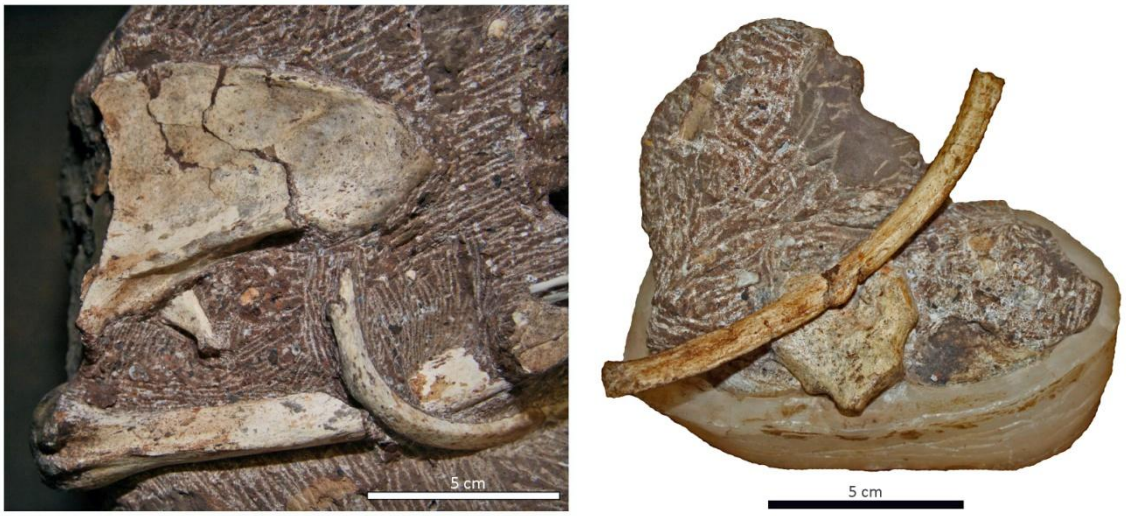



**Figure 7.11.** Left: scapula on top of the first rib (UW88-198), manubrium (UW88-172) and rib UW88-154. Right: exposed rib (UW88-154) and manubrium (UW88-172) after preparation.

Two fragmentary left teeth (UW88-19, a fragmentary upper second molar and UW88-20, a fragmentary upper third molar) were recovered *in situ*, to the right side of the "arm block". A fibula shaft fragment (UW88-202) was recovered in Facies D and attributed to MH2.

## 1.4. MH2 *ex situ* remains joining *in situ* specimens

### *1.4.1. "Scapula fragment block"*

The "scapula fragment block" (Figures 7.12 and 7.13) was found on the path used by the miners. It refits perfectly with the "arm block", through direct contact with the scapula blade (UW88-28). On the anterior face, the "scapula fragment block" contains the superior part of the right scapula (UW88-56) and the right clavicle (UW88-38) (Figure 7.12). On the posterior face it contains the right hemi-mandible fragment (UW88-54) bearing the three lower molars and a cervical vertebra (UW88-83) (Figure 7.13).


**Figure 7.12.** Upper part of the "scapula fragment block" showing the incomplete scapula fragment (bottom; UW88-56) and the right clavicle (top right; UW88-38).


**Figure 7.13.** Bottom part of the scapula fragment block showing the right hemi-mandible (UW88-54) and the cervical vertebra (UW88-83; top left corner of the block).

### *1.4.2. Mandible fragments*

Two other *ex situ* mandibular fragments join the right hemi-mandible (UW88-54): UW88-128 that bears the $P_4$ and a fragment of the $M_1$ and UW88-129, which includes $P_3$, C, $I_1$ and $I_2$. Together with the specimen UW88-54, they form the complete right mandible.

## 1.5. MH2 *ex situ* remains (provenance in the deposit unknown)

### *1.5.1. "Pelvis block"*

The "pelvis block" (UW88-B079) was identified at the site. However, it was found *ex situ*, in a mining dump, lying on the road towards the eastern part of the site. Coordinates of the location where it was recovered have been taken. The pelvis block contains the right pelvis (UW88-133), two fragments of the left pelvis (UW88-134 and UW88-135), the near complete sacrum (UW88-137), and two pieces of the last lumbar vertebra (UW88-138 and UW88-153).

### *1.5.2. "Ankle block"*

The "ankle block" (UW88-B032) is composed of the distal right tibia (UW88-97), the right calcaneus (UW88-99) and the right talus (UW88-98) on the anterior face of the block, with the pubis (UW88-52) and the femoral head (UW88-51) on the posterior face. A pelvic bone fragment (UW88-136), found in a separate block, joins the pubis (UW88-52) from the "ankle block" with the right ilium (UW88-133) from the "pelvis block" (UW88-B079).

### *1.5.3. "Thoracic vertebrae block 1"*

The "thoracic vertebrae block 1" contains two near complete thoracic vertebrae (UW88-43 and UW88-44), a thoracic vertebral fragment (UW88-114) and four rib fragments, side indeterminate (UW88-45, UW88-46, UW88-47, and UW88-48) (Figure 7.14). UW88-44 is the last thoracic vertebra and UW88-43 is the penultimate thoracic (Scott Williams, pers.comm.).

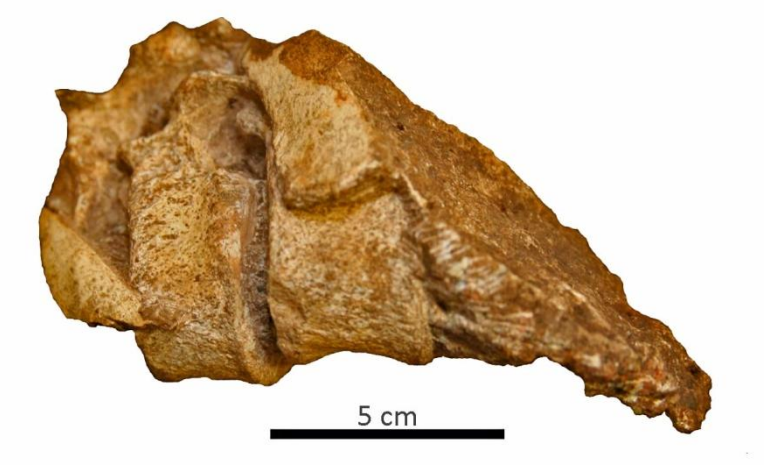



**Figure 7.14.** "Thoracic vertebrae block 1".

### *1.5.4. "Thoracic vertebrae block 2"*

The "thoracic vertebrae block 2" (UW88-B742) contains four near complete thoracic vertebrae (UW88-188, UW88-189, UW88-190 and UW88-191), from rank ¾ (UW88-188) to rank 6/7 (UW88-191) (Scott Williams, pers.comm.); a first metatarsal, side indeterminate (UW88-181); a possible sesamoid (UW88-180); a distal pedal phalanx, side indeterminate (UW88-179); the distal part of the left second rib (UW88-187); the left proximal end of the second rib (UW88-178); and two unidentified bone fragments (UW88-183 and UW88-185).

### *1.5.5. "Lumbar vertebrae block"*

The "lumbar vertebrae block" is composed of a sacral fragment (UW88-125), the last lumbar vertebral body (UW88-126), and the antepenultimate lumbar vertebral body (UW88-127). This group joins to the "thoracic vertebra block 1" (UW88-43, UW88-44, and UW88-114).

### *1.5.6. Other remains*

The left hemi-mandible is in two pieces, in direct contact with each other (UW88-55, a left fragment including $M_3$ and UW88-55b, a left fragment with a tooth root fragment).

The left fibula is in two pieces found separately, but which refit perfectly, these being the proximal shaft (UW88-23) and the medial shaft (UW88-84). The following specimens were recovered in different *ex situ* blocks and are separated from one another:

- The glenoid part of the left scapula (UW88-104) and the left acromion process (UW88-103).

- The left humeral head (UW88-101).

- The left distal femur (UW88-87).

- The left lateral end of the clavicle (UW88-94).

- Two pelvic bone fragments, including the left ischiopubic ramus with partial pubic symphysis (UW88-10) and a pelvic fragment (UW88-136).

- Elements of long bones including a right fibula shaft fragment (UW88-146), the distal end of a right fibula (UW88-65) and a proximal left tibia epiphysis (UW88-24).

- Rib fragments, which amount to two intermediate rib fragments (UW88-192 and UW88-193) found in the same block (UW88-B1003), side indeterminate and two intermediate rib fragments, side indeterminate (UW88-209 and UW88-210) found in two different blocks.

- A fragment of a cervical vertebra (UW88-96).

- A left metacarpal (UW88-182) from block UW88-B894.

- An unidentified hand bone (UW88-157).

- A proximal pedal left phalanx (UW88-91).

- Three carpals: the left capitate (UW88-150), hamate (UW88-106) and triquetral (UW88-107).

- A molar crown fragment (UW88-201).

## 2. POSITION, DIRECTION AND INCLINATION OF *IN SITU* HOMININ BONES

### 2.1. MH1: cranial remains and metatarsals

The MH1 *in situ* cranial specimens are not very informative in terms of direction and angle: the teeth were recovered during sieving, and even though their location within the deposit is known, their orientation is not. The orientation of the two vault fragments and the two metatarsals was not recorded when they were collected from the deposit.

### 2.2. MH2: "arm block"

#### *2.2.1. Position in the deposit*

The original position of the block within the deposit is known. It was found with the proximal humerus and scapula sticking out of the matrix toward the south. The corner of the block facing north contains the hand bones and the distal femur. All the bones found in the arm block are on the top of the block, which is facing toward the opening of the cave.

#### *2.2.2. Direction*

Inside the block, there is a general tendency for the long bones to be orientated along the same south-north axis (proximal part of the bone facing south and distal part facing north) (Figure 7.15). This is the case for the right scapula, humerus, radius, ulna and femur, for the metacarpals II, III, IV and V, and for the complete intermediate rib (UW88-61). The other ribs have different orientations: SE-NW for the first rib, NW-SE for the second rib and W-E for the partial ribs UW88-59 and UW88-60. The thumb phalanx is orientated E-W, the first metacarpal is orientated upside down with its proximal extremity facing north and the distal extremity facing south, the third phalanx is orientated SW-NE and the fourth and fifth phalanges are orientated N-S. It is noteworthy that only the smallest bones (phalanges) and the curved bones (ribs) do not follow the general north-south direction.

### *2.2.3. Inclination*

The general inclination of by the bones inside the arm block is between 20 and 30° relative to the horizontal plane (Figure 7.15). This is true for the following bones, which are all in the same plane: the scapula and humerus (orientated with their distal side inclined toward the top of the deposit and their proximal side toward the bottom of the cave), other long bones (i.e. femur, radius and ulna) and ribs.

**Table 7.1.** Direction and inclination of the MH2 skeletal elements present in the arm block.

| SPECIMEN | ELEMENT | DIRECTION | INCLINATION |
|---|---|---|---|
| UW88-28 | right scapula | S-N | 30° |
| UW88-57 | right humerus | S-N | 30° |
| UW88-63 | right femur | S-N | 30° |
| UW88-85 | right radius | S-N | 25° |
| UW88-62 | right ulna | S-N | 20° |
| UW88-61 | intermediate rib | S-N | 30° |
| UW88-198 | first right rib | SE-NW | 30° |
| UW88-58 | second right rib | NW-NE | 30° |
| UW88-59 | intermediate rib | W-E | 30° |
| UW88-60 | rib fragment | W-E | 30° |
| UW88-119 | first right metacarpal | N-S | 100° |
| UW88-118 | second right metacarpal | S-N | 55° |
| UW88-117 | third right metacarpal | S-N | 60° |
| UW88-116 | fourth right metacarpal | S-N | 60° |
| UW88-115 | fifth right metacarpal | N-S | 120° |
| UW88-160 | first right phalanx | E-W | 120° |
| UW88-164 | second proximal right phalanx | - | - |
| UW88-120 | third proximal right phalanx | SW-NE | 30° |
| UW88-108 | fourth proximal right phalanx | N-S | 110° |
| UW88-121 | fifth proximal right phalanx | N-S | 70° |
| UW88-123 | second intermediate right phalanx | E-W | 110° |
| UW88-161 | third intermediate right phalanx | - | - |
| UW88-122 | Right fourth intermediate phalanx | N-S | 50° |
| UW88-162 | fifth intermediate right phalanx | - | - |
| UW88-124 | first distal right phalanx | N-S | 50° |
| UW88-198 | first right rib | SE-NW | 30° |
| UW88-58 | second right rib | SE-NW | 30° |
| UW88-61 | intermediate rib | SE-NW | 30° |
| UW88-59 | intermediate rib | W-E | 30° |
| UW88-60 | rib fragment | W-E | 30° |

The metacarpals and phalanges have various inclinations: the second, third and fourth metacarpals have an inclination relative to the horizontal of 55°, 60° and 60° respectively and the first metacarpal has an inclination of 100° relative to the horizontal plane. The fifth metacarpal is in a different plane and has an inclination of 120°. The phalanges have various inclinations, from 30° to 120° (Table 7.1). Only the smallest bones (phalanges and metacarpals) are not in the same 20°-30° inclination plane.


**Figure 7.15.** Orientation and inclination of the bones from the arm block.

## 3. POSITION, DIRECTION AND INCLINATION OF HOMININ REMAINS INSIDE *EX SITU* BLOCKS

Except for the MH1 skull, which contains sediments providing stratigraphic information, it is impossible to assess the orientation, position and angle within the site of the specimens recovered in *ex situ* blocks, since the position of the blocks within the deposit is unknown. Therefore, only the position, direction and inclination of the specimens relative to other within the same block are discussed here.

### 3.1. MH1: skull

The CT-scanning and 3D rendering of the MH1 skull provides a mean by which to explore inside the vault. The skull is filled with sediments arranged in parallel bedded layers, which are aligned obliquely inside the calvarium (Figure 7.16). It is possible to identify two different types of sediments. On the left side of the skull, the sediment is slightly lighter in colour and present more coarse grains, while on the right side it is more homogenous, darker in colour and composed of finer grains. There is a slight unconformity between these two types of sediments in the form of cavities (black holes in Figure 7.16). The layering on the left occurs at an angle to the layering on the right and the layering on the right appears to truncate the layering on the left above the initial deposit. Observations of the sediments filling the calvarium (Figure 7.16) suggest that MH1 skull was lying on its left side and partly filled with sediment at the time of the initial deposition, whilst its other half (the right side, now broken) was still sticking out above the initial deposit. This initial infill must have occurred at an angle to the horizontal, as indicated by the sediment lapping on the skull wall. The skull was subsequently filled by sediments that deposited inside the cave in a horizontal fashion, which is also visible inside Pit 1 (P. Dirks, pers. comm.). The unconformity visible inside the skull was also observed during the preparation of the “skull block” and is present on top of the block B051. It is interpreted as a bedding surface, possibly the top of Facies D. It suggests that

MH1 was lying in a horizontal fashion, and following an east-west orientation along the north wall of the pit (P. Dirks, pers. comm.).

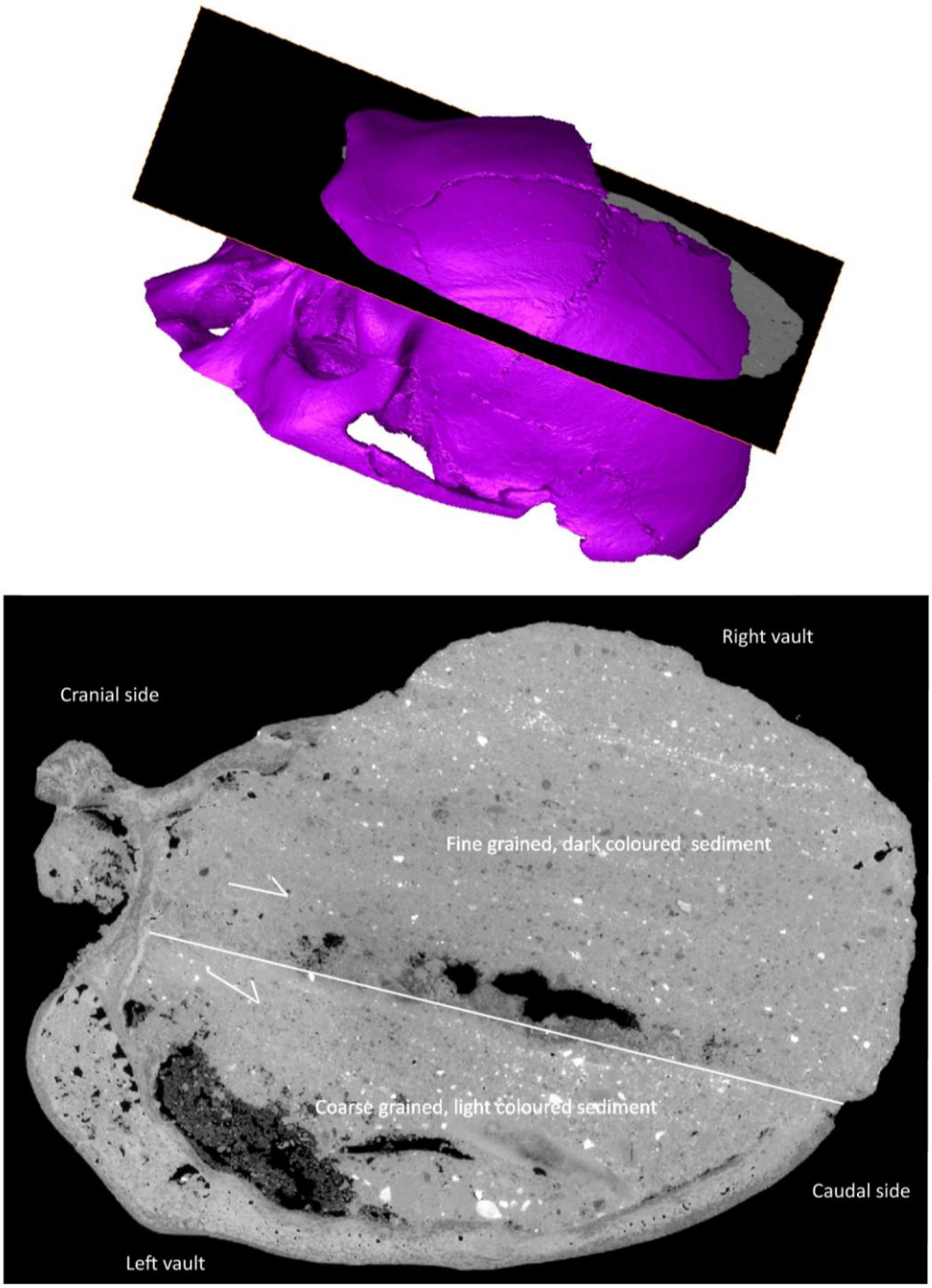



**Figure 7.16.** Cross-section (view from the top, see image of the top illustrating where the orthoslice is taken from) of the skull showing the sediments inside the vault (the white line indicates the limit between the two types of sediments, and the white arrows indicate the inclination of the sedimentary laminae) (images: courtesy of K. Carlson, modified).

### 3.2. MH1: bones from the "skull block"

The position of the skull relative to the right humerus in the same block is known. They are both positioned in the same plane, with the proximal humerus facing the same direction as the anterior part of the skull. The left humeral head, also recovered in the "skull block", is orientated perpendicular to the right humeral shaft.

### 3.3. MH1: bones from the "clavicle block"

The relative position of the mandible and ulna is known. They are orientated in the same plane and are parallel to each other; the long axis of both bones follows the same direction with the distal part of the ulna and the anterior part of the mandible facing in the same direction. The other remains have a shape that does not allow the attribution of a direction or inclination (i.e. cervical and thoracic vertebrae, distal radius fragment, pelvic fragments and calcaneum).

### 3.4. MH1: bones from block B051

Twelve elongated hominin bones have been identified inside block UW88-B051, including a complete femur, a complete clavicle, four ribs, a fibula shaft, two shafts of long bones (possible humerus and tibia or distal femur), a distal ulna, the shaft of a possible radius or rib, and the left mandible. They are all in the same plane. The general same orientation can be noticed for the femur, the fibula, the tibia/distal femur, the possible humerus, the right ulna, the ribs, and the mandible. Only the clavicle and the shaft of the rib/radius are perpendicular to the other bones (see Figures 7.7 and 7.8).

### 3.5. MH2: *ex situ* remains

MH2 remains present in the various *ex situ* blocks ("ankle block", "pelvis block", "thoracic vertebrae blocks" 1 and 2) cannot be assigned a direction or inclination. In each case, there is only one bone or no bone for which the shape allows an estimation of direction and inclination.

## 4. GENERAL ORIENTATION OF THE GEOLOGICAL UNIT (FACIES D)

Flowstone 1, which underlies Facies D, dips towards the north. Therefore, it is proposed that the sediments making up Facies D were accreted from south to north. Immediately below the position of the MH1 *in situ* vault fragments, there is a horizontal layer with many rounded fragments showing internal laminations reminiscent of cross bedding (Figure 7.17). This also indicates a flow from the south to the north or north-west (P. Dirks, pers.comm.).

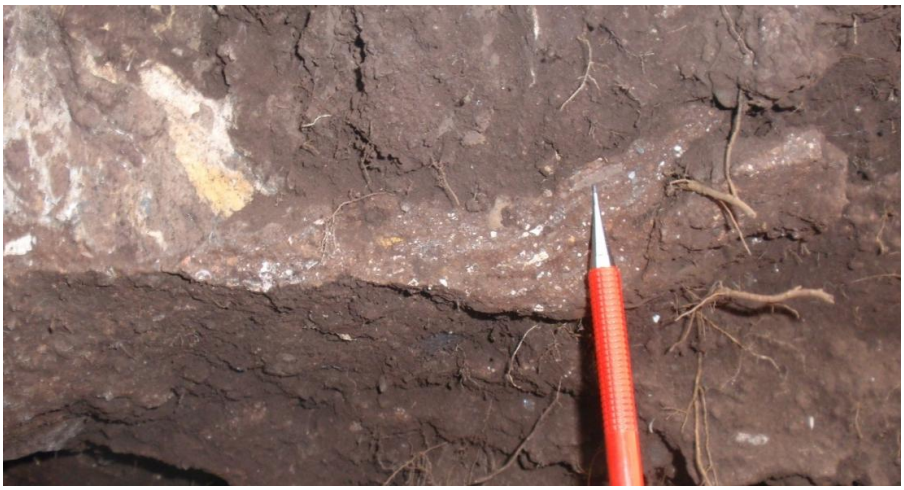


**Figure 7.17**. Layer overlying Facies D, below where the MH1 vault fragments were recovered. Note the horizontal lamination of the sediments, reminiscent of cross-bedding (image: courtesy of P. Dirks).

## 5. TRANSPORT AND MOVEMENT OF THE HOMININ REMAINS

### 5.1. Distances between MH1 remains

#### *5.1.1. 3D distance between the vault fragments and the incisor and canine*

The vault fragments were found together and consequently given the same coordinates. The incisor and canine were found nearby. All the remains are almost at the same height (the teeth are only 4 cm above the vault fragments) and are 21 cm apart in the horizontal plane, which indicate a slightly oblique displacement of the cranial remains compared to the teeth. The 3D distance between the teeth and the vault fragments is:

$= \sqrt{[(80313.0035 - 80313.2021)^2 + (2865448.2352 - 2865448.4410)^2 + (1442.9496 - 1442.9990)^2]} = \sqrt{[(-0.1986)^2 + (-0.2058)^2 + (-0.0494)^2]} = \sqrt{(0.0394 + 0.0423 + 0.0024)}$

$= \sqrt{0.0841} = 29$ cm

*5.1.2. 3D distance between the metatarsals and the vault fragments*

$= \sqrt{[(80313.0035 - 80311.7103)^2 + (2865448.2352 - 2865448.738)^2 + (1442.9496 - 1443.293)^2]} = \sqrt{[(1.2932)^2 + (-0.5028)^2 + (-0.3434)^2]} = \sqrt{(1.6724 + 0.2528 + 0.1179)} = \sqrt{2.0431} = 142$ cm

MH1 is considered to have almost reached its adult size (Berger *et al*., 2010). *Au. africanus* has a stature estimated at 138 cm for the males (McHenry, 1991). *Au. sediba* is considered to fall within this range (Berger *et al*., 2010). This implies that the top of the skull and the feet should be about 138 cm apart in the anatomical position. The distance observed in the site between the vault fragments and the metatarsals is 142 cm, which is consistent with the normal distance expected between these elements in the case of a body lying with the legs fully extended.

*5.1.3. Movement affecting specimens found in* ex situ *blocks*

In *ex situ* blocks, there is little displacement of the bones from their anatomical position. The "clavicle block" is composed of elements of the upper right body that are anatomically close to each other: the right clavicle, mandible, acromion, ulna and distal radius, along with some fragments of the right pelvis. The only exceptions are a piece of the left pelvis. The two vertebrae (one cervical and one thoracic) present in the "clavicle block" belong to the upper body. In the "skull block", there are also elements from the right side: the skull, humerus and femur. The ilium and proximal left humerus head are the only elements from the left side. Inside the "clavicle" and "skull blocks", the remains are very close to each other, or even in direct contact with one another in some cases (e.g. the mandible is in contact with the ulna). The maximum distance observed inside a block

containing MH1 remains is between the ilium and the distal humerus (only 20 cm). The presence of numerous elements of MH1 on the same plane inside block B051 confirms that little movement has affected the skeleton. This block preserves bones from both the upper (clavicle, ribs, mandible, ulna, possible radius and humerus) and the lower body (femur and fibula) and from the right (ulna) and the left (femur, clavicle and mandible) side. Furthermore, the possibility of refitting between the "clavicle block" and the block B051 proves that most elements of MH1 are constrained in a small volume of sediment, and were preserved close to each other, even though no direct articulation is present.

## 5.2. Distances and direction of transport between the MH2 remains

### *5.2.1. Estimation of distances*

All the *in situ* MH2 remains have been found in the same clastic calcified sediment block (the "arm block") and show little evidence of transport. Bones of the upper part of the body (i.e. scapula, manubrium, first rib and humerus) are preserved in anatomical position, and some of them are still in contact with one another (the scapula is touching the manubrium and first rib). The radius and ulna have been displaced and moved towards the south and slightly toward the west. This movement has placed them next to the humerus, parallel to this bone on its left side. The same has happened to the femur, which is at the same level as the distal part of the radius and ulna, on the western part of the arm block, together with the knee. The movement that has affected the radius, ulna and femur occurs along a double axis (north-south and east-west). The right femur has been slightly displaced toward the west (left part of the "arm block"), but this would be valid only if the right leg was straight and aligned with the rest of the body. If the right leg was flexed with the knee pointing west, then there is no lateral displacement of the femur. The position of the right leg will be discussed further on (see paragraph 7. Hominin remains refitting). One rib shows evidence of a lateral movement in the western part of the block: the second right rib (UW88-58), which has been displaced to the left of the scapula. This rib has also been rotated from its original position since the vertebral end is

now facing left (opposite to the anatomical position). The intermediate complete right rib UW88-161 is in a position that is anatomically correct, on top of the humerus. Concerning the rib fragments UW88-59 and 60, it is difficult to assess whether or not they have been displaced, since they have not been attributed a side. If they are fragments of right ribs, then they would have been displaced toward the west of the block, together with the second right rib. On the other hand, if they are fragments of left ribs, then they are in a normal anatomical position. The first rib and manubrium are located on the dorsal side of the scapula, whereas anatomically speaking they should be on top of it (on the ventral side of the scapula). Moreover, the vertebral part of the first rib is situated near the lateral side of the scapula, whereas it should be near the medial side. The same applies to the manubrium, which is upside down compared to its anatomical position. This is consistent with a rotational movement of the first rib and the manubrium, which have turned over. There is no lateral or horizontal movement involved, but there is definitively a vertical movement as well as a twist of the bones themselves around their anatomical centre of gravity.

The fibula shaft that was attributed to MH2 is the only other *in situ* bone that was found elsewhere than in the "arm block". The coordinates of the centre of the "arm block" are the following:

$X = [X_{(\text{west corner})} + X_{(\text{east corner})}]/2 = [(-80312.8364) + (-80313.3912)]/2 = -160626.2276/2$

$X = -80313.1138$

$Y = [Y_{(\text{south corner})} + Y_{(\text{north corner})}]/2 = (2865449.2029 + 2865448.6870)/2 = 5730897.8899/2$

$Y = 2865448.9449$

For the Z coordinate, we choose the mean between the highest (east corner) and the lowest (south corner) parts of the "arm block":

$Z = [Z_{(\text{south corner})} + Z_{(\text{east corner})}]/2 = (1442.1930 + 1442.5105)/2 = 2884.7035/2$

Z= 1442.3517

The distance between the fibula shaft fragment and the centre of the “arm block” is:

= √ [(80313.1138 – 80316.5110)$^2$ + (2865448.9449 – 2865448.5060)$^2$ + (1442.3517 – 1444.0560)$^2$] = √ [(-3.3972)$^2$ + (0.439)$^2$ + (1.704)$^2$] = √ (11.5409 + 0.1927 + 2.9036) = √ 14.6372 = 3.8259 m

*5.2.2. Estimation of the movement inside MH2 “arm block”*

Anatomically, the proximal radius and ulna are just below the distal humerus. In the “arm block”, the proximal radius has been pushed toward the proximal humerus and is 16 cm away from the distal humerus. The same applies to the ulna, which, in the “arm block”, is 21 cm away from the distal humerus.

The distance between the distal femur and the distal humerus in their anatomical position (all limbs fully extended) is the equivalent of the length of the complete femur plus more or less ¾ of the length of the radius. This is estimated based on the 3D reconstruction of MH2 in her anatomical, standing upright, position (Figure 7.18). The anatomical distance between the distal humerus and the distal femur is 47.5 cm (Figure 7.18).

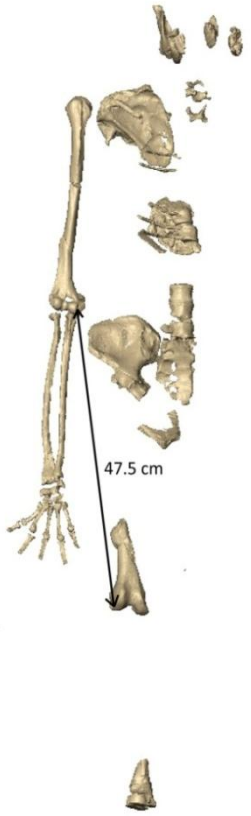



**Figure 7.18.** Distance distal humerus to distal femur (reconstruction of MH2 skeleton in upright posture.

The distance between the distal femur and the distal humerus inside the "arm block" is 14 cm. This means that the femur has been displaced by: 47.5 – 14 = 33.5 cm. Whether the leg was flexed or straight, the distal femur is still orientated in the same direction as the humerus, which means that the femur itself was in its straight position (distal part facing the lower body).

The hand bones (carpals, metacarpals and phalanges) are all located right below the radius and ulna and therefore respect their normal anatomical position.

The second right rib has been displaced from its original anatomical position. Anatomically, the distance between the vertebral end of the second rib and the medial side of the scapula should be very low, since they occupy a very small space. If a natural flattening of the rib cage was the only process that had happened, the second rib should be lying on top of the scapula. Here, the lateral distance between the vertebral end of the

second rib (medial side) and the scapula is 10.1 cm (Figure 7.19), which means that another type of movement has affected the second rib.

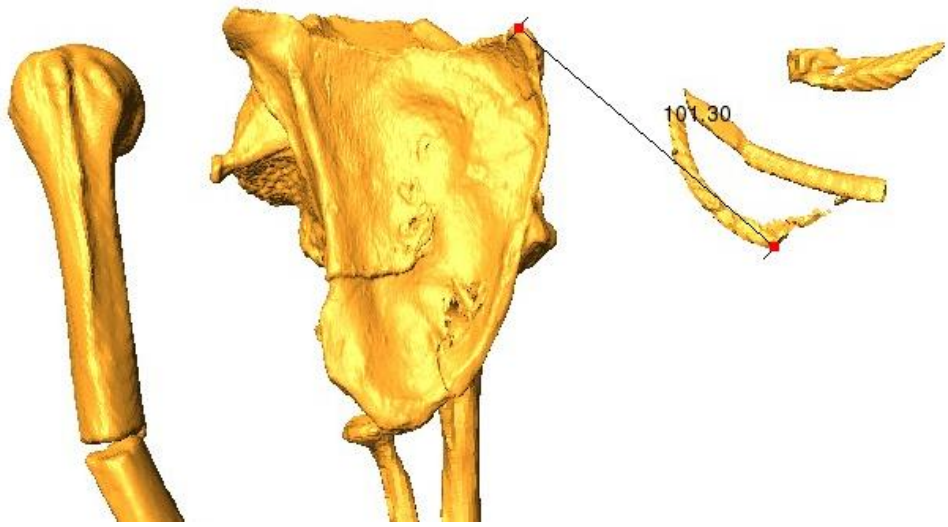



**Figure 7.19.** Distance between the medial side of the scapula and the vertebral end of the second right rib.

In the other *ex situ* blocks, there is also evidence for little movement: the ilium is associated with the pelvis (block UW88-B079) and the right ankle was found associated with the right femoral head and pubis.

## 5.3. Distance MH1-MH2 remains

### *5.3.1. 3D distance between MH1 vault fragments and north corner of the "arm block"*

$= \sqrt{[(80313.0035 - 80312.9041)^2 + (2865448.2352 - 2865448.6870)^2 + (1442.9496 - 1442.4860)^2]} = \sqrt{(0.0994^2 + 0.4518^2 + 0.4636^2)} = \sqrt{(0.0098 + 0.2041 + 0.2149)} = \sqrt{0.4288} = 65.5$ cm

### *5.3.2. 3D distance between MH1 vault fragments and south corner of the "arm block"*

$= \sqrt{[(80313.0035 - 80313.1473)^2 + (2865448.2352 - 2865449.2029)^2 + (1442.9496 - 1442.1930)^2]} = \sqrt{[(-0.1438)^2 + (-0.9677)^2 + (0.7566)^2]} = \sqrt{(0.0207 + 0.9364 + 0.5724)} = \sqrt{1.5295} = 123.7$ cm

*5.3.3. 3D distance between MH1 vault fragments and west corner of the "arm block"*

= √ [(80313.0035 – 80312.8364)$^2$ + (2865448.2352 – 2865449.0068)$^2$ + (1442.9496 – 1442.3037)$^2$] = √ [(0.1671)$^2$ + (-0.7716)$^2$ + (0.6459)$^2$] = √ (0.0279 + 0.5953 + 0.4171) = √ 1.040 = 102.0 cm

*5.3.4. 3D distance between MH1 vault fragments and east corner of the "arm block"*

= √ [(80313.0035 – 80313.3912)$^2$ + (2865448.2352 – 2865449.0019)$^2$ + (1442.9496 – 1442.5105)$^2$] = √ [(-0.3877)$^2$ + (-0.7667)$^2$ + (0.4391)$^2$] = √ (0.1500 + 0.5878 + 0.1928) = √ 0.9308 = 96.5 cm

*5.3.5. 3D distance between MH1 metatarsals and north corner of the "arm block"*

= √ [(80311.7109– 80312.9041)$^2$ + (2865448.738– 2865448.6870)$^2$ + (1443.293– 1442.4860)$^2$] = √ [(-1.1938)$^2$ + (0.051)$^2$ + (0.807)$^2$] = √ (1.4251 + 0.0026 + 0.6512) = √2.0790 = 144.2 cm

*5.3.6. 3D distance between MH1 metatarsals and south corner of the "arm block"*

= √ [(80311.7103 – 80313.1473)$^2$ + (2865448.738 – 2865449.2029)$^2$ + (1443.293 – 1442.1930)$^2$] = √ [(-1.437)$^2$ + (-0.4649)$^2$ + (1.1)$^2$] = √ (2.0650 + 0.2161 + 1.21) = √3.4911 = 186.8 cm

*5.3.7. 3D distance between MH1 metatarsals and west corner of the "arm block"*

= √ [(80311.7103 – 80312.8364)$^2$ + (2865448.738 – 2865449.0068)$^2$ + (1443.293 – 1442.3037)$^2$] = √ [(-1.1261)$^2$ + (-0.2688)$^2$ + (0.9893)$^2$] = √ (1.268 +0.0723 + 0.9787) = √2.3191= 152.3 cm

*5.3.8. 3D distance between MH1 metatarsals and east corner of the "arm block"*

= √ [(80311.7103 – 80313.3912)$^2$ + (2865448.738 – 2865449.0019)$^2$ + (1443.293 – 1442.5105)$^2$] = √ [(-1.6809)$^2$ + (-0.2639)$^2$ + (0.7825)$^2$] = √ (2.8254 + 0.0631 + 0.6123) = √3.5008 = 187.1 cm

## 5.4. Distance with other *in situ* hominin remains

All the *in situ* hominin specimens occur inside a 110 cm high vertical plane (i.e. distance from the lowest point, which is the east corner of the arm block, to the highest point, which is the position of MH1 metatarsals). The only exception is the fibula which is outside of this area, at a distance of 186 cm away from the eastern corner of the arm block, in the Z plane. Horizontally, the hominin specimens are more spread out. Along the X axis (west-east direction), there is 589 cm between the MH2 fibula shaft fragment, which is the most western specimen and the MH6 mandible which is the most eastern specimen recovered to date. Along the Y axis (north-south direction), the most northern specimen (the MH6 mandible) and the most southern one (corner of the arm block) are 725 cm apart from one another. The MH1 and MH2 specimens are all very close to each other, if one excludes the fibula shaft attributed to MH2. They are included in a very small volume of 0.85 cubic metres (excluding the fibula shaft fragment), calculated as follows:

Volume of sediment containing the *in situ* hominin remains = side x side x side, or:

X (longest distance between MH2 "arm block" and MH1 metatarsals) x Y (longest distance between MH2 "arm block" and MH1 metatarsals) x Z (longest distance between MH2 "arm block" and MH1 metatarsals) = (80313-3912 – 80311.7103) x (2865449.2029 – 2865448.738) x (1443.293-1442.1930) = 1.68 x 0.46 x 1.1 = 0.85 cubic metres.

The following table (Table 7.2) summarizes the different distances between MH2 and MH1 remains, between the "arm block" and the MH1 vault fragments and between the "arm block" and the MH1 metatarsals.

**Table 7.2**. Distances between *in situ* MH1 and MH2 remains.

| Element | Distance (cm) |
|---|---|
| Distance MH1 vault fragments and incisor | 29 |
| Distance MH1 vault fragments and metatarsals | 142 |
| Distance “arm block”-fibula shaft (UW88-202) | 383 |
| Distance “arm block” north corner-MH1 cranial remains | 65 |
| Distance “arm block” south corner-MH1 cranial remains | 124 |
| Distance “arm block” west corner-MH1 cranial remains | 102 |
| Distance “arm block” east corner-MH1 cranial remains | 96 |
| Distance “arm block” north corner-MH1 metatarsals | 144 |
| Distance “arm block” south corner-MH1 metatarsals | 187 |
| Distance “arm block” west corner-MH1 metatarsals | 152 |
| Distance “arm block” east corner-MH1 metatarsals | 187 |

## 6. POSITION, DIRECTION, ORIENTATION AND MOVEMENT OF THE *IN SITU* HOMININ REMAINS: SUMMARY

A few important conclusions can be drawn from the analysis of spatial organisation of the hominin bones found *in situ*. The general inclination of MH2 remains is slightly oblique (inclination of 20-30°) going from the top to the bottom of the deposit (Figure 7.20). The upper part of the body is facing south. There is no evidence for major horizontal displacement, only for slight movement from south to north and for slight lateral movement to the west as shown by a few remains in the “arm block”. There are also some movements of rotation observed for the first and second right ribs and the manubrium. The *in situ* MH1 and MH2 remains are very close to each other in the three planes (XZ, YZ and XY) (Figure 7.20). The transport rate is low for both MH1 and MH2, meaning either that the bones have not been displaced very much or that the skeletons were transported and deposited while still more or less fully articulated. The case of the MH2 fibula, which is almost 4 metres away from the “arm block”, seems to be an exception rather than the rule. It is suspected that this specimen might belong to another individual (see Chapter 9. Reattribution of some remains). The MH1 metatarsals are also far from the other MH1 and MH2 remains. If they do belong to MH1, they are 142 cm away from the *in situ* vault fragments, which is anatomically logical only if the body is aligned with the legs and feet

towards the west of the deposit. Their attribution to MH1 will be discussed later (see Chapter 9). The geology shows a general south to north dip direction for Facies D, interpreted as the general direction of the debris flow. This seems to be also visible in the organisation of the sediments present inside the MH1 skull, which shows inclined laminae indicative of south to north accretion. Consequently, the skull should be repositioned lying left lateral down and facing north.

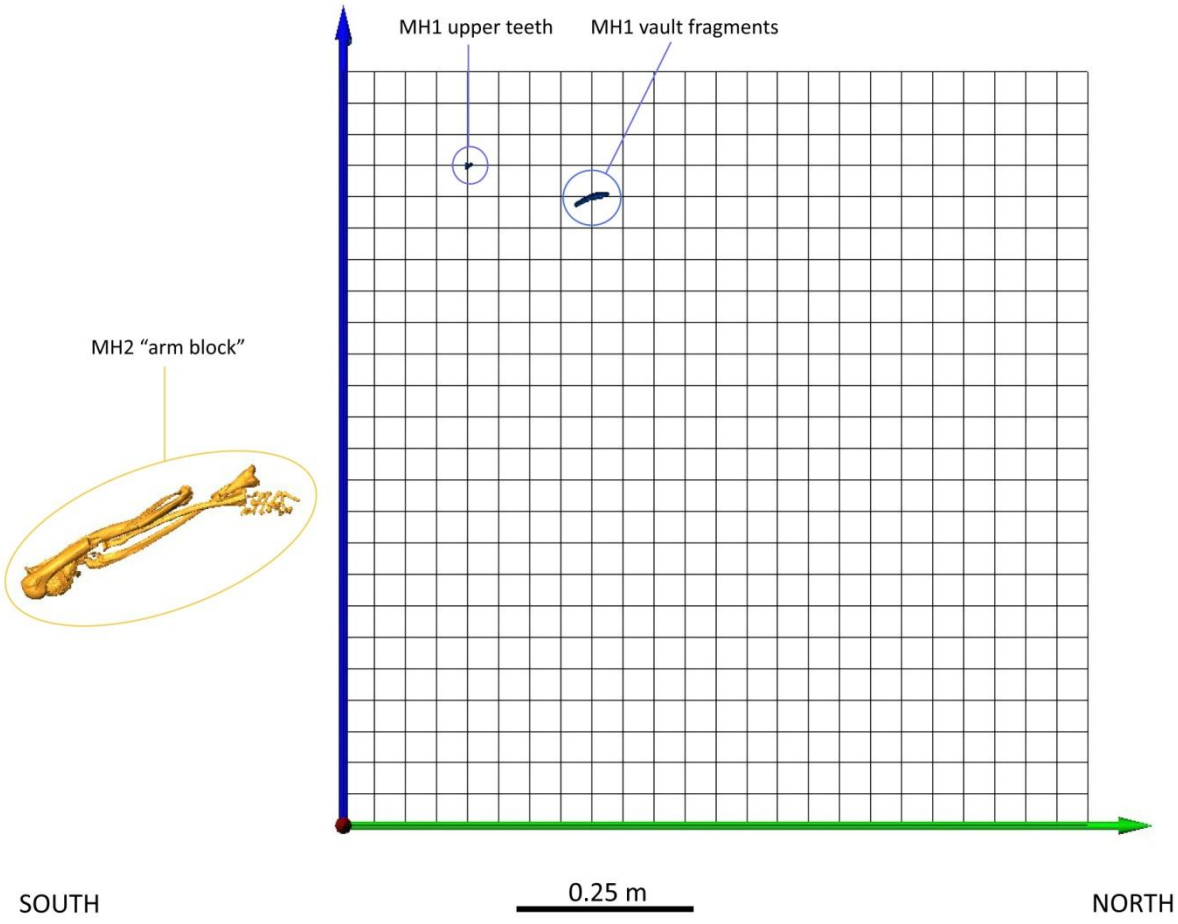



**Figure 7.20.** Inclination of the "arm block" inside the deposit and distance between the MH1 and MH2 *in situ* remains.

These different conclusions serve as guidelines and clues to propose refitting hypotheses for the *ex situ* hominin remains (see Chapter 4 for more details about the refitting methods).

## 7. REFITTING OF HOMININ REMAINS

### 7.1. Positioning the reference points and other *in situ* remains

The exact coordinates and orientation of the arm block are known, it is therefore used as the reference point for the 3D model. The Avizo software positioned automatically the vault fragments, the teeth and the metatarsals, using their coordinates. The vault fragments and the incisor and canine are positioned just above the arm block, slightly to the east. The metatarsals are on the western side and higher up in the deposit (Figure 7.21).

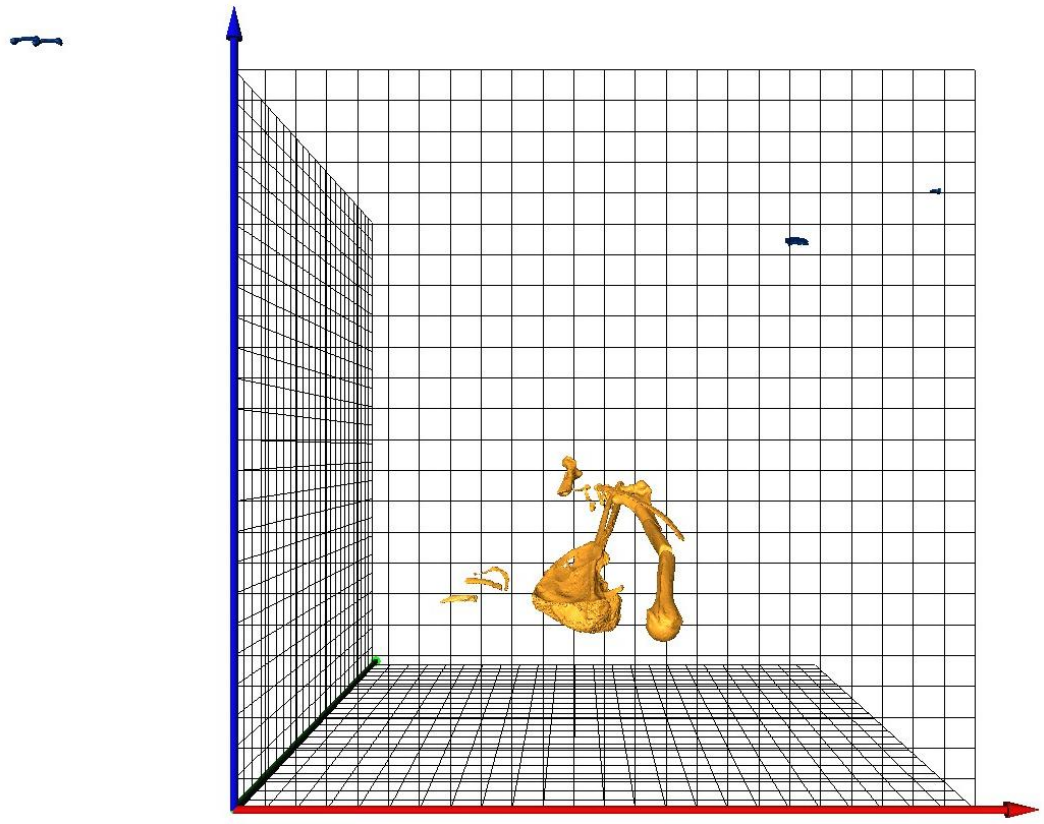


**Figure 7.21.** All *in situ* remains in the grid (XZ view). MH1 remains are represented in blue, MH2 remains in orange.

## 7.2. Refitting MH1 remains

### *7.2.1. Step 1: joining the "skull block" and the "ilium block"*

The distal right humerus was sticking out of the ilium block and was most probably broken by a mining blast. This implies that it was still attached to the correspondent humeral shaft (from the "skull block") when the fossilisation and sedimentation processes took place. The two pieces, once manually removed from the sediment, connect perfectly. It is therefore possible to refit them, together with the different elements found in the two blocks (in other words, the distal humerus and ilium in one hand with the skull and humeral shaft on the other hand). The "skull block" and the "ilium block" can therefore be refitted back into the deposit as a single unit (Figure 7.22).

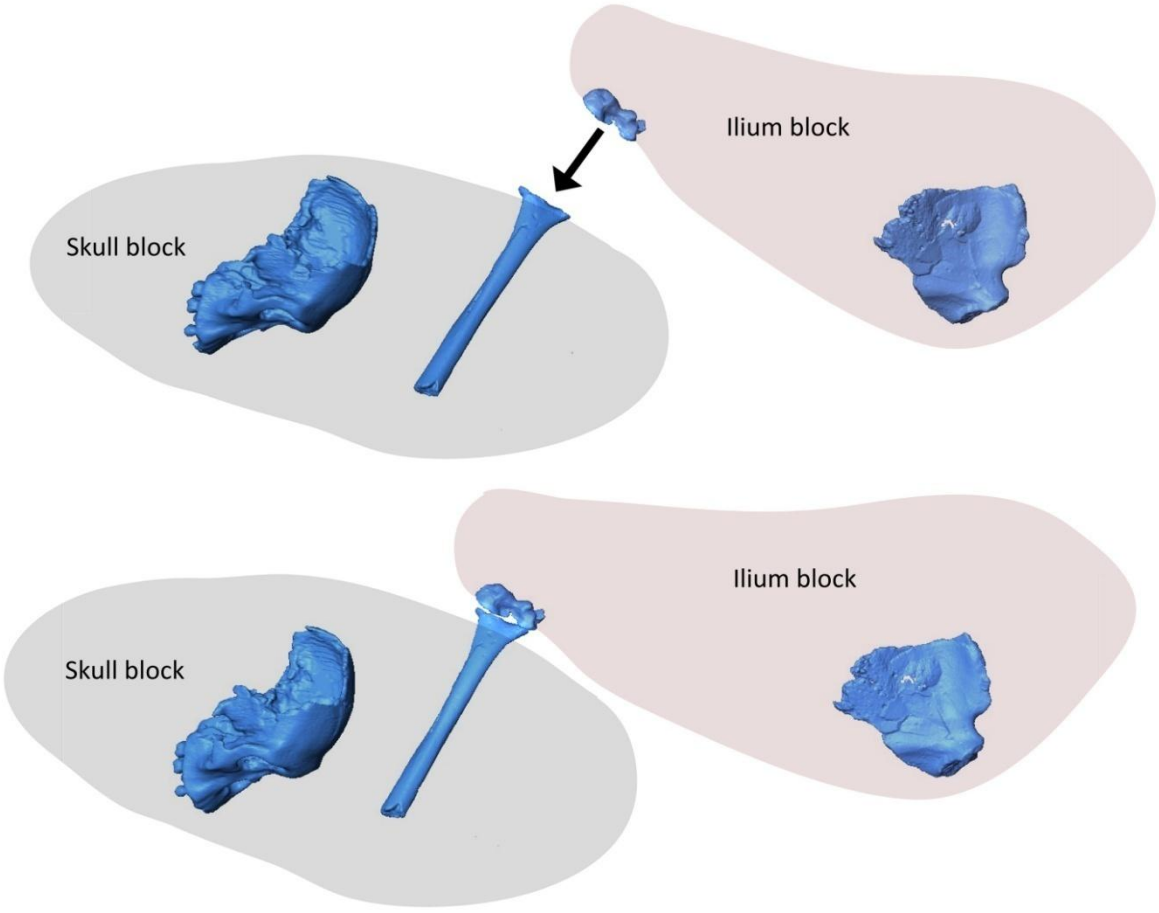



**Figure 7.22.** Refitting of the "skull block" and the "ilium block".

### *7.2.2. Step 2: refitting the "skull" and "ilium blocks" into the deposit*

The morphology of the deposit and of Facies D imposes limitations in terms of the position of the *ex situ* remains, both on the horizontal and vertical planes. In the vertical plane, the position of the remains is constrained on top by the upper limit of Facies D (just above the *in situ* MH1 vault fragments and teeth) and by the presence of the MH2 "arm block" below. In the horizontal plane, the position of the remains is constrained by the wall of the cavity for the Y coordinate and by the edges of Facies D for the X coordinates. All the bones (skull, humerus and ilium) have to be positioned in a volume removed by the miners. Moreover, I have demonstrated previously the low movement rate for both MH1 and MH2 skeletons and between the two individuals themselves. It is therefore likely that the MH1 skull and associated remains come from an area near the vault fragments and the teeth.

The skull is lying on its left side and with a slight inclination of 15° as shown by the sediments located against the left wall of the skull (see the synchrotron images, showing the layering of the sediments in the skull, Figure 7.16). The geology indicates that the general direction of the flow that is associated with the washing of Facies D goes from south to north, which is also visible in the way the sediments in the calvarium are sloping down away from the face. This implies that the skull should be facing north. This information (orientation of the sediment inside the calvarium) is considered as direct evidence for the orientation of the skull, with consequently a maximum probability for the skull to be orientated with its face towards north. Hence, the most likely position for the group skull-humerus-ilium is consistent with the skull lying on its left side, facing north, below where the vault fragments and teeth were found (Figure 7.23). It is located above the "arm block". The humerus is therefore orientated with its proximal part toward the north-east and its distal part toward the south-west. The ilium is on the western part, at the same height as the "arm block" (Figure 7.23 and Appendix 7). The position of the group skull-humerus-ilium in the deposit is based on an indirect argument for the position

(i.e. the proximity with the vault fragments and constraints of the limits of Facies D) and has therefore a probability lower than one. In other words, the exact position of these bones could be modified toward the west and/or higher or lower in the deposit, within the limits of the geological unit.

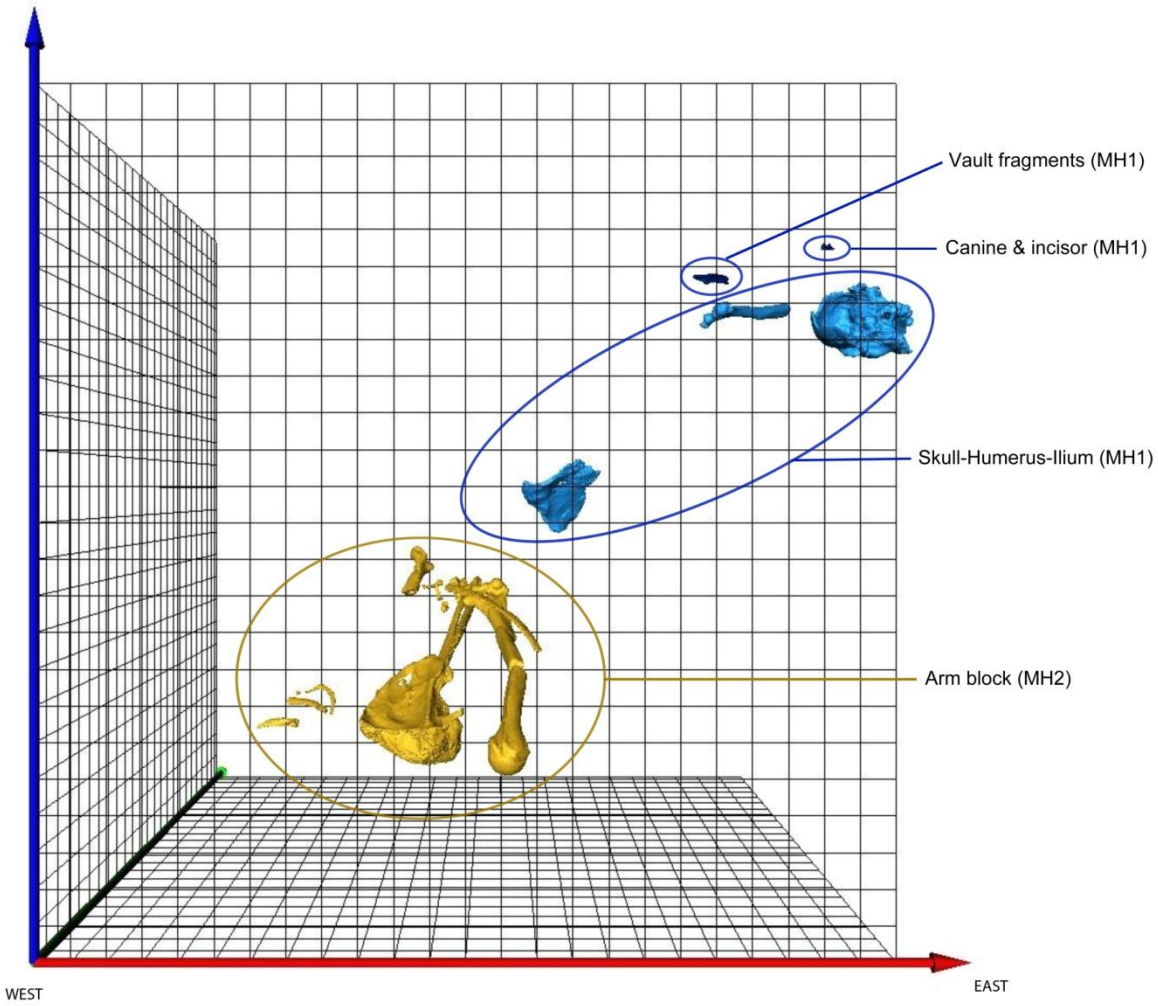



**Figure 7.23.** Refitting of the group skull-right humerus-left ilium (MH1) in the deposit (view from the south).

### *7.2.3. Step 3: refitting the "clavicle block"*

From there, it is possible to propose a hypothetical position for the bones recovered inside the "clavicle block". The position of the mandible (two fragments, UW88-2 and UW88-8), cervical (UW88-9) and thoracic vertebrae (UW88-11), ulna (UW88-3),

right acromion (UW88-113), distal radius (UW88-12) and rib fragment (UW88-13) in relation to each other is known (Figure 7.24). The position of the clavicle (UW88-1) is estimated based on the photographs of both sides of the block. There is no record of the position and orientation of the pelvis fragments; their exact placement inside the clavicle block is therefore hypothetical.

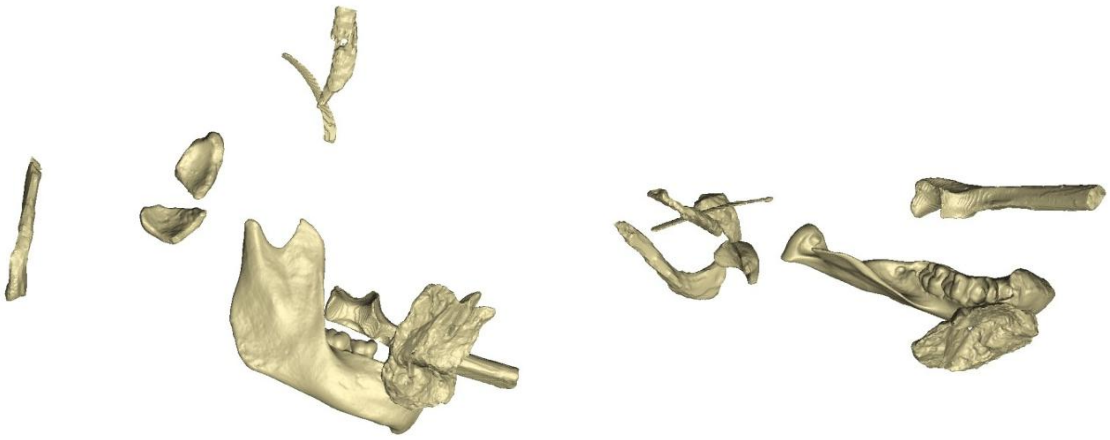


**Figure 7.24.** MH1 clavicle and associated bones in their original position in the "clavicle block" (left: lateral view; right: superior view).

The complete right hemi-mandible and near complete ulna are used as clues to refit the "clavicle block" with the group skull-humerus-ilium. The other remains (i.e. vertebrae, acromion and distal radius) are too small and/or very fragmentary, and they do not have an elongated shape that could be used as an indicator of movement direction or angle.

There is no evidence for an important vertical movement in the deposit and the position of the "clavicle block" is constrained by the limit of Facies D at the top and the presence of the "arm block" at the bottom. It is reasonable to conclude that the "clavicle block" has to be at the same level or above the skull. Given the inclination of the MH1 humerus, it seems that the remains of that individual are positioned in a horizontal plane. It is suggested that the ulna, clavicle and mandible should therefore also be positioned horizontally. Three possible variations for the position of the "clavicle block" are considered:

- upper arm straight or flexed
- no movement compared to the anatomical position versus displacement
- rotation of the ulna (and associated bones) on itself

The combination of these three variations leads to a maximum of 16 possible hypotheses (Table 7.3).

**Table 7.3**. List of possibilities concerning the position of the "clavicle block".

| Hypothesis | Position upper arm | Movement | Rotation ulna |
|---|---|---|---|
| **1** | straight | no | no |
| **2** | straight | no | yes |
| **3** | straight | yes, to the east | no |
| **4** | straight | yes, to the east | yes |
| **5** | straight | yes, to the west | no |
| **6** | straight | yes, to the west | yes |
| **7** | straight | yes, to the south | no |
| **8** | straight | yes, to the south | yes |
| **9** | flexed | no | no |
| **10** | flexed | no | yes |
| **11** | flexed | yes, to the east | no |
| **12** | flexed | yes, to the east | yes |
| **13** | flexed | yes, to the west | no |
| **14** | flexed | yes, to the west | yes |
| **15** | flexed | yes, to the south | no |
| **16** | flexed | yes, to the south | yes |

Hypothetical cases with the arm straight and no rotation of the ulna (i.e. hypotheses 1, 3, 5 and 7) have a low probability, because of the position of the mandible, which is orientated in the opposite direction to the skull. Whether the "clavicle block" has been displaced (as in hypotheses 3, 5 and 7) or is near the "skull block" (as in hypothesis 1), it is difficult to explain how the mandible would have moved from its anatomical position, attached to the skull and therefore with its anterior side facing north, as the skull is, to a position completely opposite, with the anterior side facing south and the lingual side facing the top of the deposit. This would imply a strong movement that would have detached the mandible from the skull, completely flipped it over and rotated it 180°.

The hypotheses consistent with the arm flexed, rotation of the ulna, some movement (12, 14 and 16) or no movement (10) are also not very likely, because, as in hypotheses mentioned above, they imply that the mandible has flipped over and rotated 180° and is now facing in the opposite direction to the skull.

Hypotheses with the arm extended and rotation of the ulna, with movement (hypotheses 4, 6 and 8) or without movement (hypothesis 2), are considered as possible. The mandible has not flipped over as in cases mentioned above, but only rotated 180°.

The hypotheses consistent with the arm flexed, no rotation of the ulna and some movement (11, 13 and 15) are also considered as possible; they do not imply any rotation of the mandible.

Finally, when considering all the different data and by applying an elimination process, hypothesis 9 (arm flexed, no movement, no rotation) is the one that has the highest probability to be the correct one. All the hypotheses with the arm straight and no rotation of the ulna (1, 3, 5 and 7) and with the arm flexed and rotation (10, 12, 14 and 16) have been ruled out because of the position of the mandible with its lingual side facing the opening of the cave. The other *in situ* remains indicate very little evidence for movement. I therefore retain a case scenario with no movement, over other possible cases scenarios with movement such as hypotheses 4, 6, 9, 11, 13 and 15. I also assume that little movement would have affected the mandible, which should still be in its anatomical position (in other words, hypothesis 2 can be ruled out). Finally, the “skull block”, where the humerus was found, is very narrow (Figures 7.25 and 7.26), which allows the placement of the “clavicle block” really close to the “skull block” in the z axis.

**Figure 7.25**. MH1 skull and right humerus embedded in the block. Note the narrowness of the calcified sediment below the humerus. Scale = 10 cm.

Consequently, I suggest that scenario 9 has the highest probability, and so the "clavicle block" was located just below the "skull block", with the proximal ulna facing south in a position consistent with the arm flexed. The position of the different pelvis fragments (UW88-6, 7 and 14) in the block has not been recorded. Given the overall small size of the "clavicle block", I propose that the pelvis elements must be in very close association with the group ulna-clavicle, whether below or above, to the left or to the right.

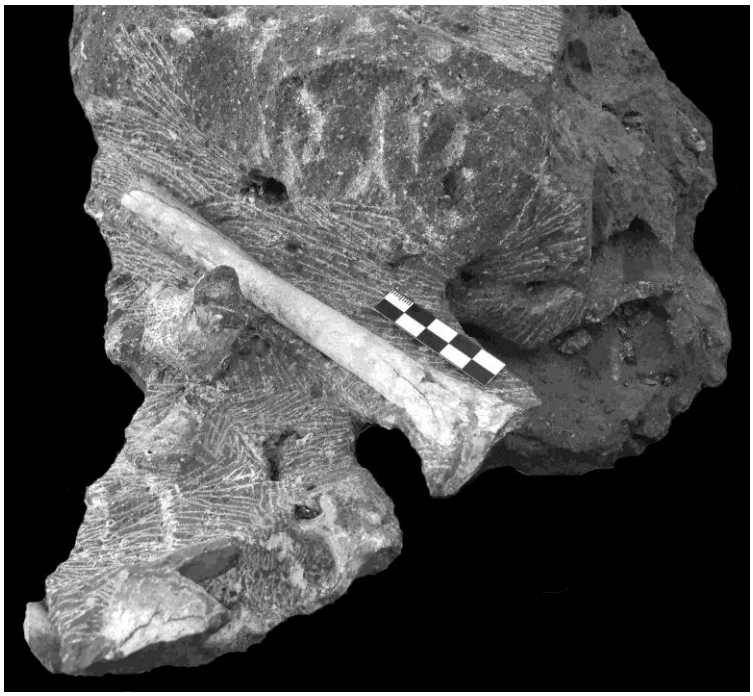


**Figure 7.26.** MH1 right humerus, in block. Note the thinness of the block below the humerus. Scale bar = 5 cm.

### *7.2.4. Step 4: refitting the right femur*

The femoral shaft fragments come from an isolated *ex situ* block. Given the general movement observed for the refitted elements of MH1 (skull, humerus, ulna, clavicle), it is proposed that the femur is lying horizontally. In order to be consistent with the position of the right metatarsals and given the low movement rates of his remains, it seems more likely that the femur should be orientated with its distal part towards the metatarsals, in other words facing west. Both horizontal and vertical displacement from an anatomical position are considered as possible: to the east (no further east than the ilium given the morphology of the deposit; if it was the case, the femur would still be in a non-excavated part of the deposit), the west or the south in the horizontal plane and to the bottom of the deposit in the vertical plane. Movement to the north and to the top of the deposit are not possible, they would place the femur out of the facies and/or out of the excavated area.

Consequently, the position of the femur is conditioned by the following variables:

- Anatomical position of the leg: straight versus flexed
- Rotation: femur in anatomical position versus flipped (the femur can have any side – anterior, posterior, medial or lateral- facing the top of the deposit)
- Horizontal displacement: no movement versus movement (to the east, the west, the south)
- Vertical displacement: no movement versus movement down the bottom of the deposit

This leads a total of 2 (leg straight or leg flexed) x 4 (anterior, lateral, posterior or medial side facing the top of the deposit) x 4 (no horizontal movement, movement to the west, the east or the south) x 2 (no vertical movement or vertical movement toward the bottom) = 64 combinations.

Any of these hypotheses present the same level of probability. If there is some movement, the femur should not be too far from the group skull-humerus-ilium. The general position retained for the upper body (group skull-humerus-ilium and "clavicle block") seems to indicate an orientation toward the SSW. In that case, the femur should be on the eastern side of the deposit, close to the ilium. However, the metatarsals are on the opposite side and they argue in favour of the leg orientated toward the east, in which case the femur should be on the east of the upper body, facing east. It seems difficult to decide which of these hypotheses is more likely. For the femur, I propose to define a hypothetical area in which that specimen comes from. This area goes from the top of Facies D to above the arm block for the z coordinate, from the ilium to the metatarsals for the x coordinate and from the vault fragments to the southern part of the "arm block" for the y coordinate.

### *7.2.5. Refitting the bones from block UW88-B051*

Since the bones present inside this block have not been prepared yet, it is for the moment not possible to include them in the 3D reconstruction. It is, however, possible to

propose how they would refit with the other specimens. The distal right ulna and the left mandible preserved inside the block B051 refit directly with the proximal right ulna and the left canine from the "clavicle block". From there, it is possible to propose the following refitting hypothesis for the block B051 and the bones it contains. The most likely refitting hypothesis for the "clavicle block" (see above) is consistent with the arm flexed, no rotation and no movement. If one positions the broken distal ulna and the left mandible from block B051 accordingly, then the left femur is orientated along the body, on the south of the skull, with the proximal part facing southwest, and the distal part facing northeast. The ribs are between the skull and left femur; the left clavicle is next to the distal part of the left femur and therefore close to the right ulna and the right mandible, and presents the same orientation as the right clavicle, northwest-southeast. The left mandible is below the right humerus and close to the right mandible, with the anterior part pointing northeast (see Figure 8.4 in the following chapter).

## 7.3. Refitting MH2 remains

### *7.3.1. Step 1: refitting the "scapula fragment block"*

The scapula fragment (i.e. acromial part) refits perfectly with the rest of the scapula (i.e. blade) present in the "arm block". This fragment was found in a block that also contains a part of the right mandible (UW88-54), two teeth (UW88-19 and UW88-20), the right clavicle (UW88-38) and a cervical vertebra (UW88-83). The block was very probably detached from the main "arm block" due to a mining blast at the site. The mandible is located below the scapula fragment and orientated with its lingual side facing the bottom of the cave. The refitting of the scapula fragment and associated bones is based on a direct match with an *in situ* specimen. This constitutes direct evidence for both the position and orientation (probability of 1 or 100% for the refitting of these bones, for both their position and orientation).

### *7.3.2. Step 2: refitting the loose remains (ankle, pelvis, sacrum, vertebrae, left carpals)*

The position of the loose remains is conditioned by the position of the "arm block" in the deposit and its surroundings. Below the "arm block" and almost touching the proximal part of the scapula is the bottom flowstone. At the right of the "arm block" is a dolomitic block. Both the dolomitic block and the flowstone do not contain fossils. Therefore, the possibilities for the location of the loose remains are restricted to either the left of the "arm block" or above it.

Moreover, I have shown a low movement rate for the *in situ* and in blocks MH2 remains. This implies that the entire skeleton was in a position close to its anatomical position when it was fossilized, with all the parts either still attached or very close to each other. Consequently, the position of the loose remains should be consistent with an original anatomical relationship.

Cervical vertebra (UW88-96)

Given the close proximity of the elements of the upper axial skeleton and upper right side (manubrium, clavicle, scapula, first two ribs), it is very likely that the cervical vertebra was located in the same area, somewhere between the mandible and the scapula, likely on top of it or at the south of it, in a section that has been removed by the miners.

Position of the legs and implications for the refitting of the right ankle, sacrum and right ilium

The position of the distal right femur and right knee can be used as a clue to reconstruct the initial position of the legs. The femur is orientated with its proximal part facing SSW and its anterior part facing NNE. It was found at the north corner of the "arm block" (Figure 7.27).

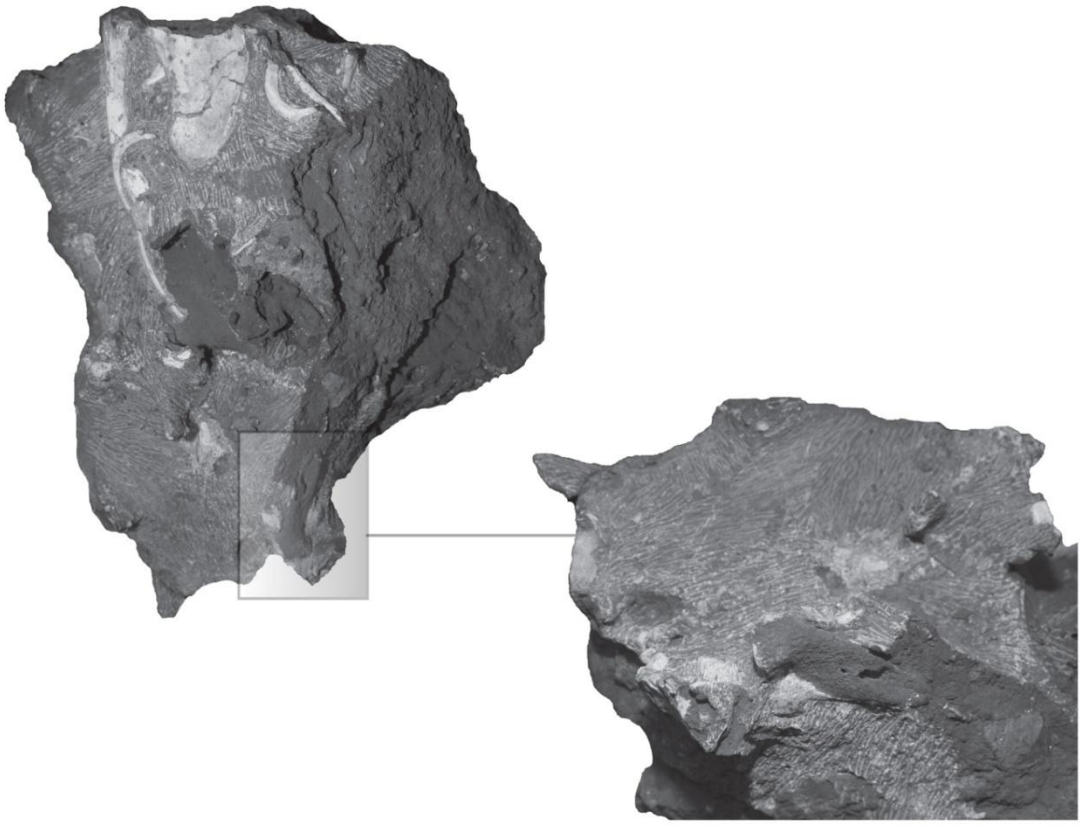


**Figure 7.27.** Position and orientation of the right femur in the “arm block”.

In other words, if the leg was fully extended, the lower part (knee, tibia, ankle and foot) would still be in the deposit. However, they have all have been recovered, which seems to indicate that the leg was not straight but flexed. This is also supported by the fact that the femur is orientated with its anterior side facing east. Moreover, the right femoral head was found associated with the right ankle. If the leg was straight, these two parts should be far away from each other. On the other hand, if the right left was flexed, then the ankle should be close to the proximal femur. It is therefore assumed that the legs were flexed, with both knees pointing east and both ankles towards the west.

If the right tibia and ankle are positioned as if the right leg is flexed on its lateral side, then the ankle should be on the left of the femur (toward the west) for the x coordinate, slightly above it since it was removed by the miners for the z coordinate, and

not further north than the distal femur for the y coordinate. It should be orientated with the distal tibia toward the distal femur (facing north) and the tarsals (calcaneum and talus) facing south-southwest.

It is possible that some movement has affected the position of the ankle from its anatomical position. Two hypotheses are retained, one without movement and one with some movement.

There is a direct join between the “ankle block” and the “sacrum block” (hypothetical orientation). According to the position of the femur and in order to be consistent with the hypothesis of the right leg being flexed, with the right knee pointing east, I suggest that the sacrum and the right ilium are lying on top of the “arm block”, somewhere between the upper limb and the distal right femur. The sacrum should be in its anatomical position (cranial part facing the top), as are the rest of the bones present in the “arm block” (except the phalanges). The ilium was found in the same block as the sacrum, on the other side of this block, it should therefore be below of it, in an anatomical position consistent with the right leg flexed toward the right.

The position of the distal femur in block shows a movement of the lower limb toward the upper part of body. Two possibilities can then be proposed regarding the position of the sacrum and right ilium:

- Hypothesis 1: a disarticulation occurred between the acetabulum and the femoral head and the lower limb was carried toward the upper body, but the sacrum and the ilium remained in their original anatomical position.
- Hypothesis 2: a disarticulation occurred between the acetabulum and the femoral head and another one occurred somewhere in the vertebral column, and both the lower right limb and the sacrum and right ilium were carried toward the upper body.

Consequently, there are two possibilities for the position of the sacrum and the ilium. They can either be in anatomical distance of the upper body (below the humerus) or, if

they have been displaced, they can be closer to the scapula. In case they have been displaced, it would make more sense to apply the same movement rate as for the femur (33.5 cm; see section 8.2.2).

"Thoracic vertebrae blocks" 1 and 2

The "thoracic vertebrae block" 1 joins the "sacrum block" (no precise information on the way it refits to it). Again, the same logic can be applied. Either the "thoracic vertebrae block" 1 is in anatomical position regarding the upper body (humerus and scapula) or it was displaced after disarticulation of the vertebral column. In this case, it should be somewhere above the humerus. The same applies to the "thoracic vertebrae block" 2. In order to be consistent with the refitting of the other loose remains, it seems more likely that the blocks 1 and 2 should be positioned according to an anatomical logic. This implies that, in the deposit, the block 1, which contains the upper thoracic vertebrae, should be closer to the upper body (scapula, first rib and manubrium) than the block 2, which contains the lower thoracic vertebrae.

Left carpals

Some elements of the right hand (distal phalanges) and the left hand are still *in situ* in the same area where the "arm block" was found, on the left (west) side of it. Therefore, the three left carpals (capitate, UW88-105, hamate, UW88-106 and lunate, UW88-107) and the left metacarpal (UW88-182) found during the preparation of *ex situ* blocks must come from this same area.

The refitting of MH2 loose remains (i.e. ankle, sacrum-ilium, two thoracic blocks and left carpals) are based on indirect arguments, namely anatomical and disarticulation logic and the observation of low movement rate for the *in situ* MH2 remains. The degree of probability of accurately refitting both their position and orientation is therefore less than 1.

## 7.4. Areas of probability for the remains

I distinguish different levels of confidence in the proposed refitting hypotheses. We can positively assess the position and orientation of MH2 scapula fragment and associated bones, since there is a direct link between them and the *in situ* remains via the broken scapula. The orientation of the group skull-humerus-ilium for MH1 can also be assessed with certainty (skull facing south and lying on its left side) since it is based on direct sedimentary data preserved in the skull itself. Its exact position in the deposit cannot be completely ascertained, although it has to be limited by the constraints of the limits of Facies D. The orientation and position of MH1 "clavicle block" as well as the position of MH2 ankle, sacrum, ilium, thoracic vertebrae have been determined based only on indirect evidence and assumptions, such as a low transport rate and an anatomical logic compared to the *in situ* bones. The hypotheses that I have retained for these remains are therefore the most likely ones but do not have a degree of probability of one. The position and orientation of the femur is the most difficult to determine.

In order to represent the different possibilities for position of the *ex situ* remains, I have summarized the different hypotheses in a diagram (Figure 7.28). Each area shows the volume in which it is possible to place them.

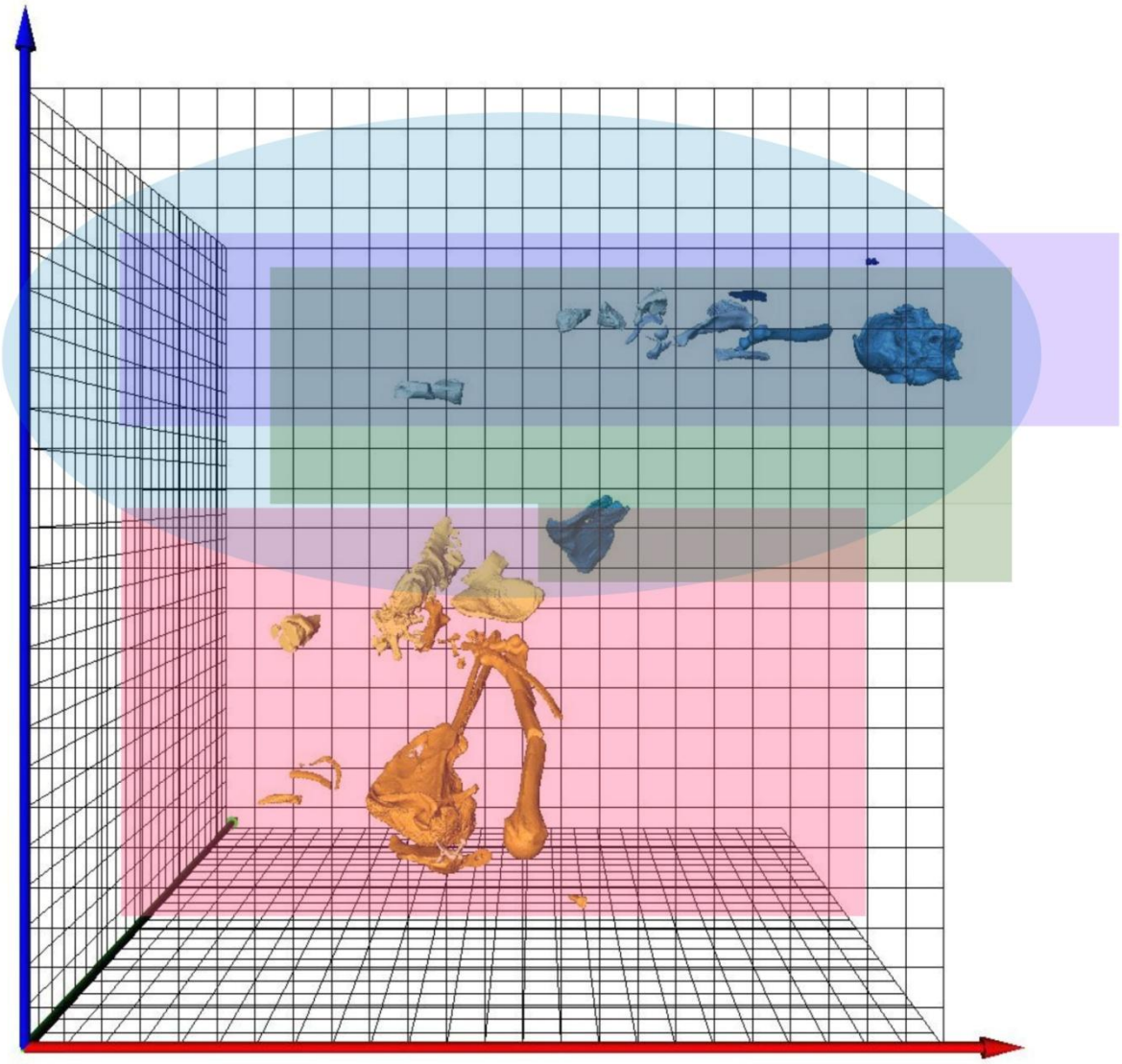


**Figure 7.28**. Different possible areas in which MH1 and MH2 remains can be refitted (green: MH1 skull-humerus-ilium; purple: MH1 clavicle block; blue: MH1 femur; pink: MH2 loose remains).

Figures 7.29 and 7.30 combine the hypothetical refitting of the hominin remains (dark golden for MH1 remains and light golden for MH2 remains) back into the deposits with stratigraphic information about the sedimentary units.

**Figure 7.29.** Hypothetical refitting of MH1 and MH2 remains within the deposit.

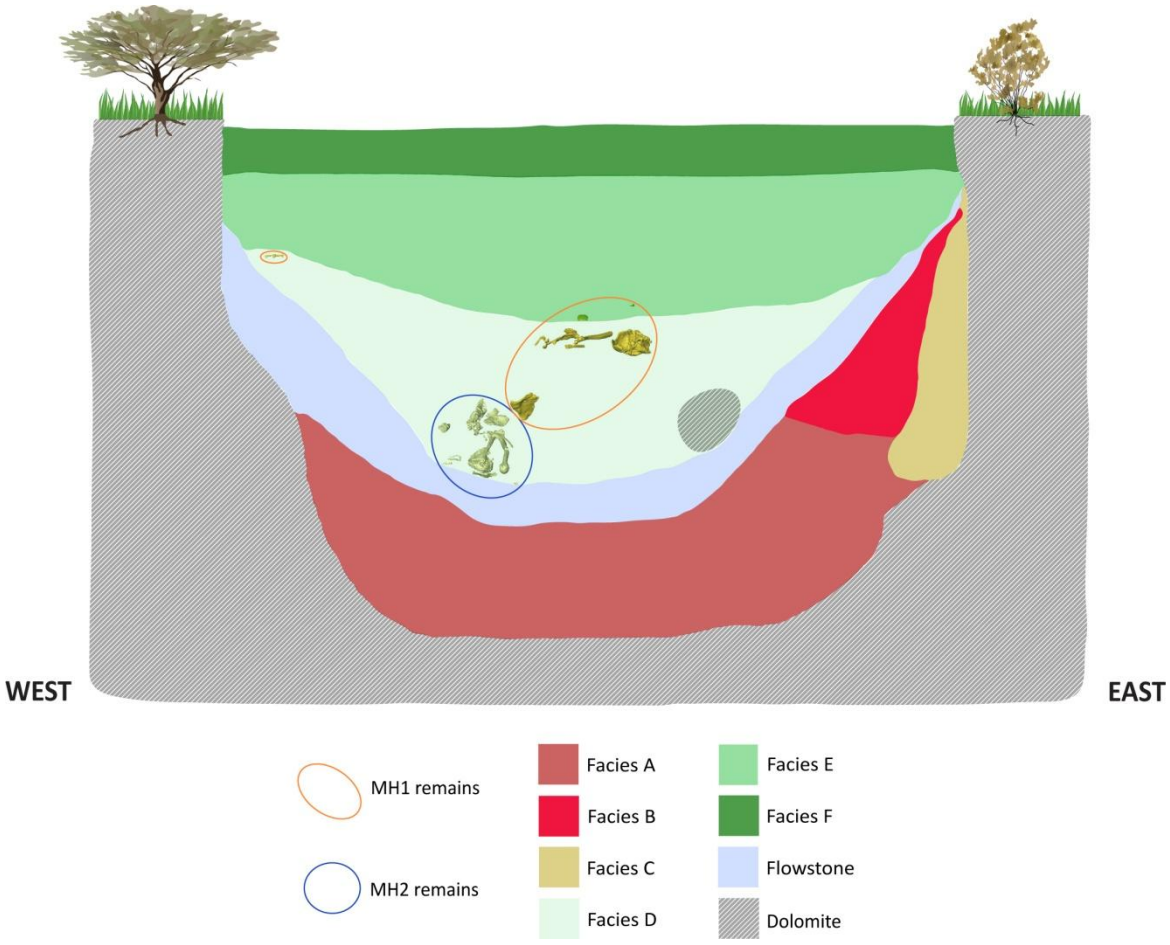



**Figure 7.30.** Simplified schematic cross-section of the position of the hominin remains inside the deposit.

## 7.5. Completion of the 3D model

Finally, the hominin remains were refitted into the 3D reconstruction of the cave deposit. The 3D model of the cave was produced by Jean Dumoncel using photographs taken after the fossils were removed from the site. The software used to reconstruct a 3D rendering of the site produces an .obj file that was then opened in Avizo 6.3 and converted into a .stl file. This .stl file was then opened in the Avizo 6.3 network containing the hominin remains and placed accordingly (Figures 7.31 to 7.34).

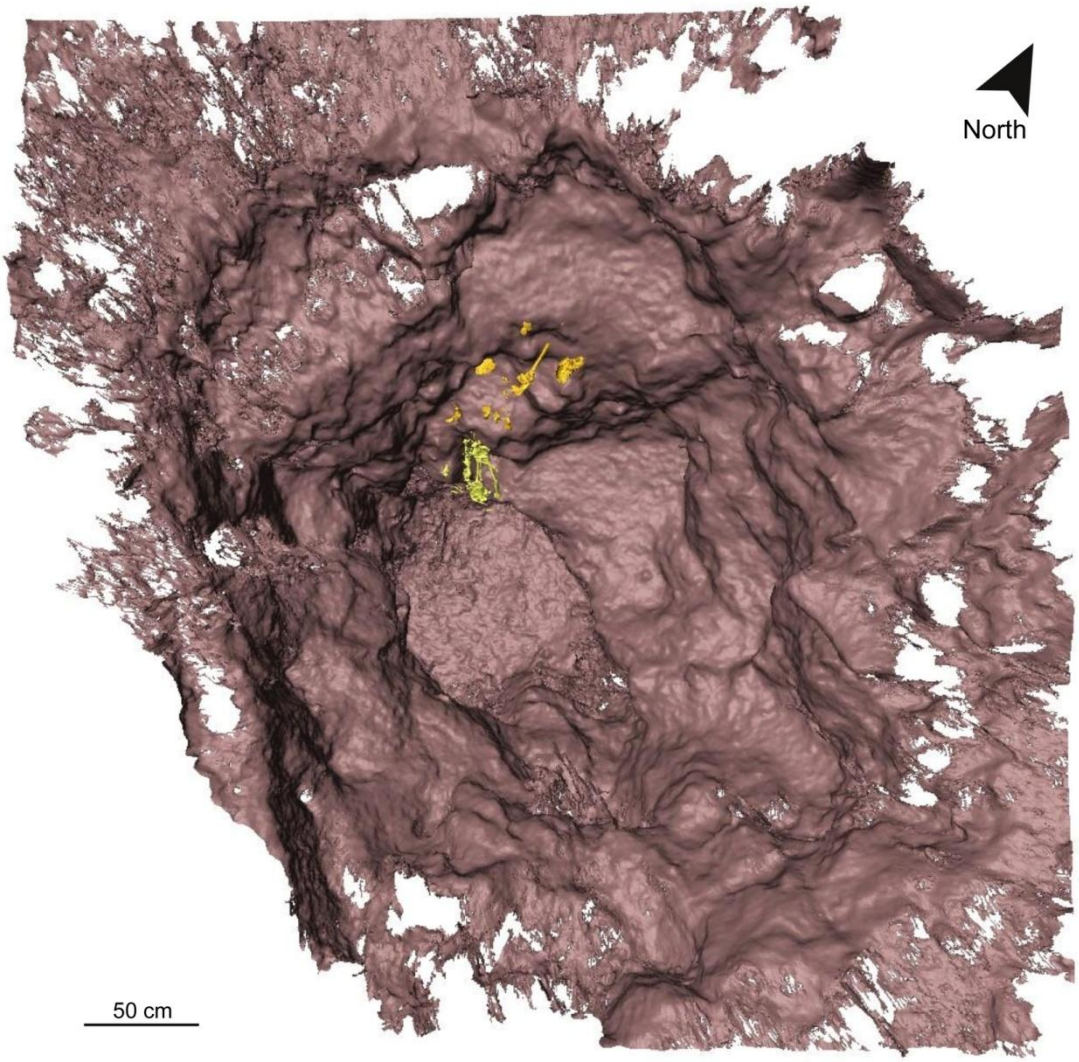



**Figure 7.31**. Final 3D reconstruction (planimetric view of the site together with the 3D renderings of MH1 and MH2 remains).

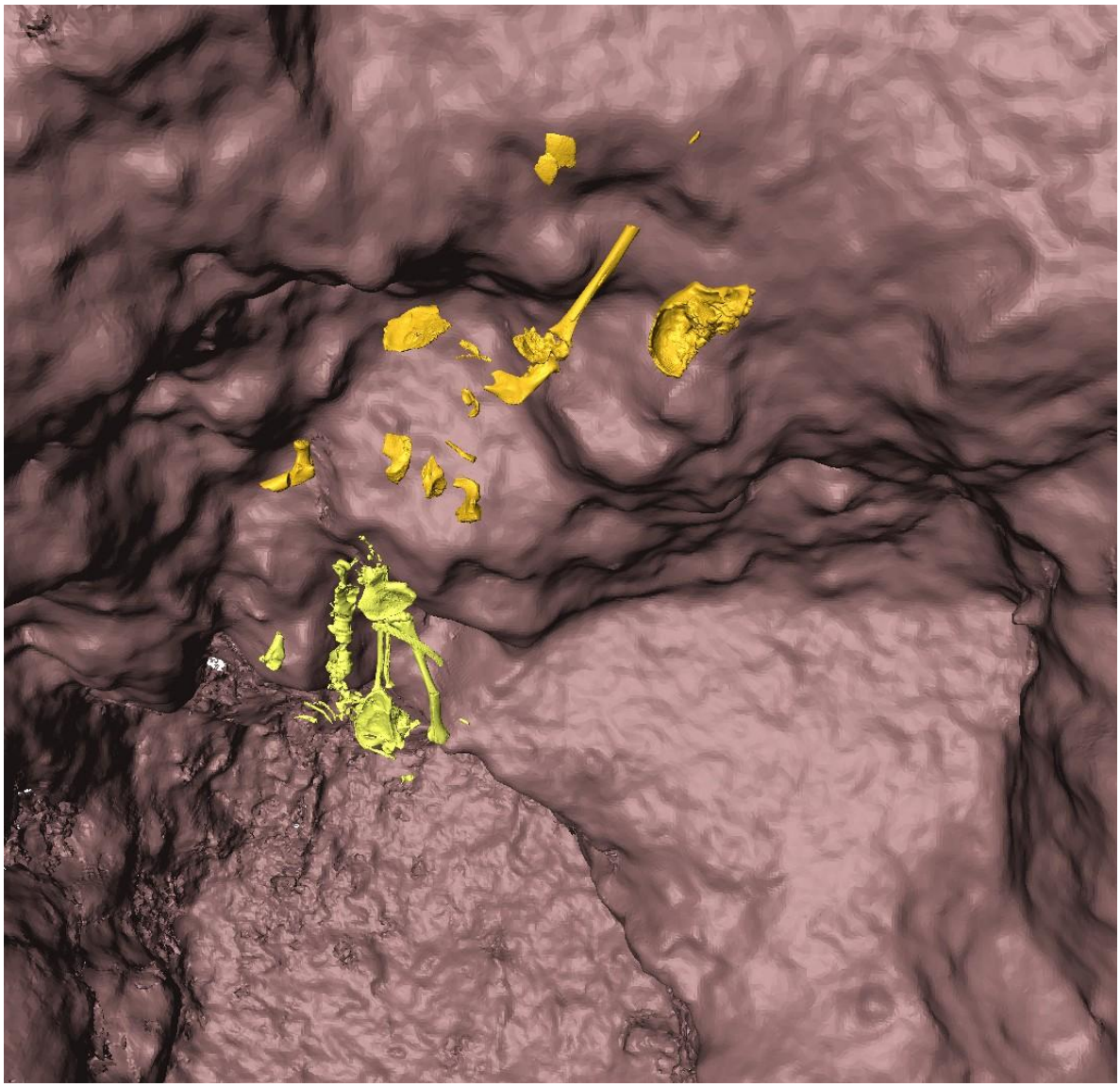


**Figure 7.32.** Close up of the hominin remains inside the deposit; plan view (dark gold on the right: MH1 remains; light gold on the left: MH2 remains).

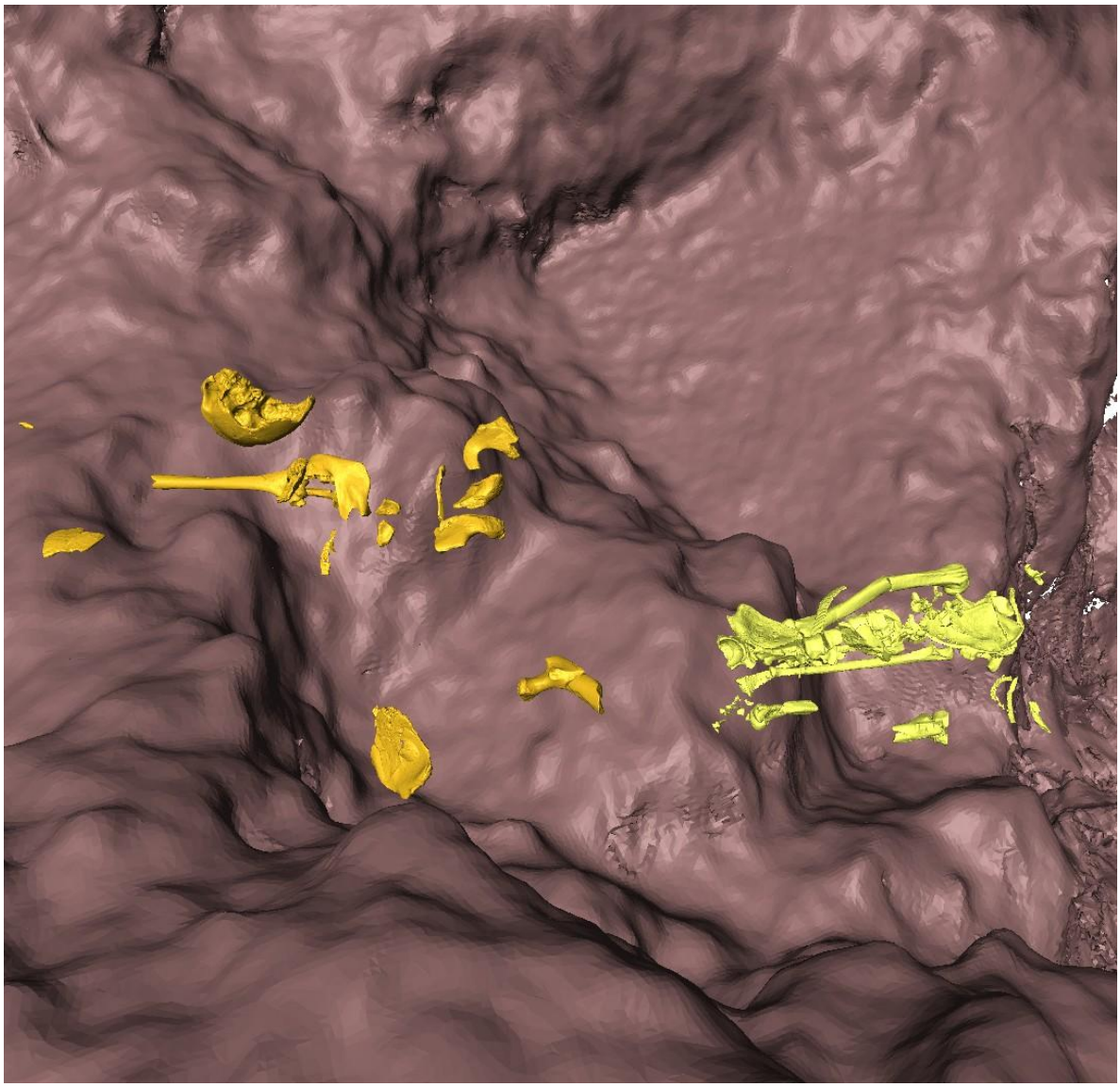


**Figure 7.33**. Close up of the hominin remains inside the deposit; north-western view (dark gold on the right: MH1 remains; light gold on the left: MH2 remains).

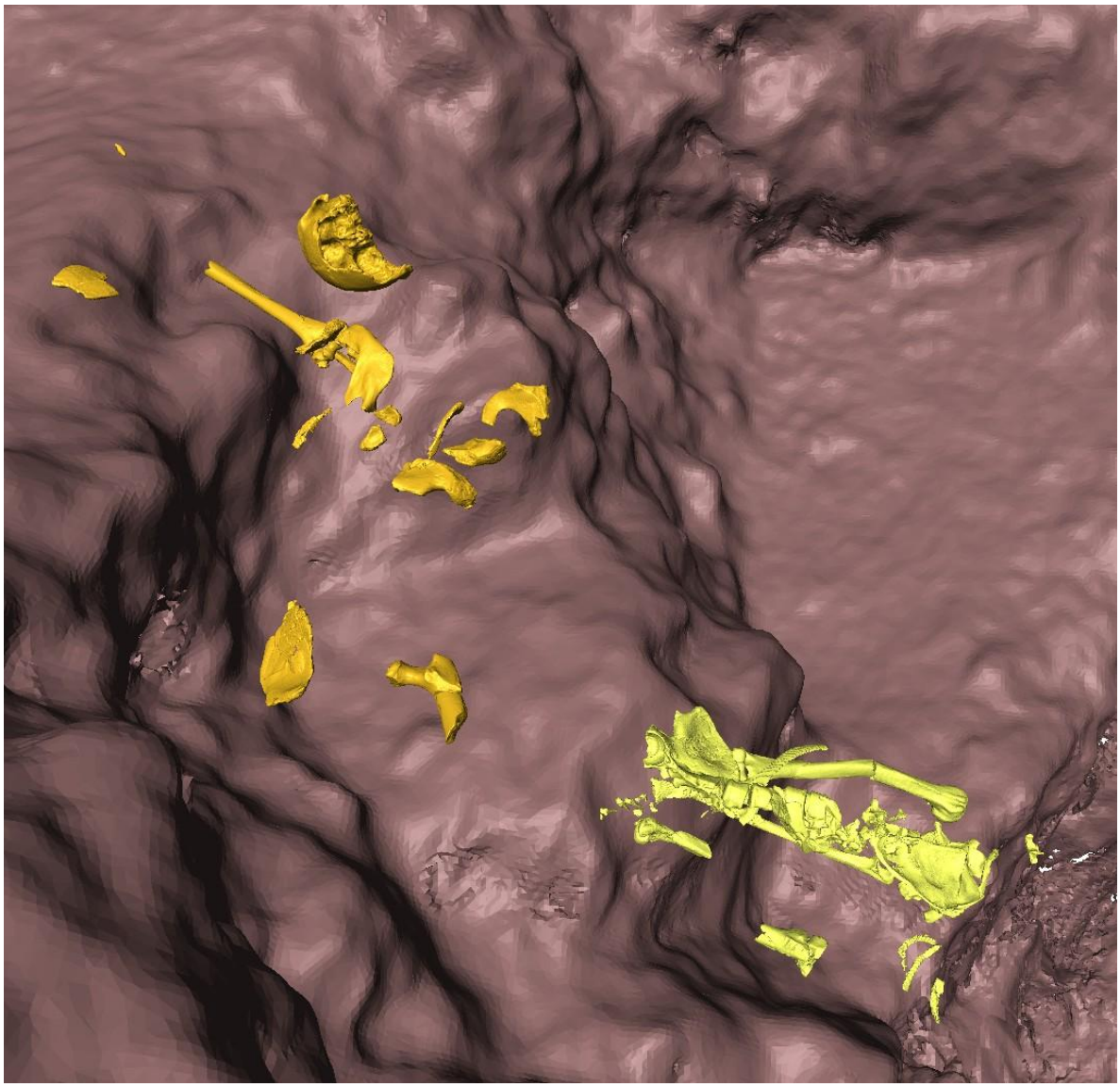


**Figure 7.34.** Close up of the hominin remains inside the deposit; western view (dark gold on top: MH1 remains; light gold at the bottom: MH2 remains).

# Chapter 8. Detailed description of the taphonomy of the hominins.

## 1. GENERAL TAPHONOMY OF THE FAUNAL ASSEMBLAGE

### 1.1. A multi-stage scenario: introduction

The Malapa fossil deposits (Pit 1 and Pit 2), in their current state, represent the lowest most strata of a cave filling, which has eroded away in the past 2 million years. That cave system was "tens of metres deep when the hominin fossils were deposited", possibly 50 to 60 metres deep (Dirks *et al*., 2010), which implies the existence at Malapa of a cave complex with deep chamber(s) 1.977 Ma years ago. Considering the extreme heterogeneity of the faunal assemblage recovered at the site in terms of bone preservation, an intricate and multi-stage taphonomic scenario has to be invoked. It is proposed that the bones of different animals, coming from different parts of the cave system (including the surface) accumulated by different biotic and abiotic agents, and were then mixed at the bottom of the cave system. The different processes likely to have contributed to the formation of the Malapa faunal assemblage are presented in detail in the following sections. The strength of the debris flow hypothesis as the main agent responsible for mixing up the bones is also discussed.

### 1.2. Primary deposit: bone accumulation in various parts of the cave system

#### *1.2.1. Contribution by carnivores*

<u>Carnivore-collected assemblage and cave use by carnivores: theoretical model</u>

Several diagnostic features inside a faunal assemblage indicate the participation by carnivores in the bone accumulation process. Hyaenid-collected assemblages are characterised by a high carnivore/ungulate ratio (>20%, in NISP: Klein and Cruz-Uribe, 1984, or in MNI: Cruz-Uribe, 1991; Pickering, 2002; Lacruz and Maude, 2005), and a significant fragmentation ratio (NISP/MNE, 4.9: Richardson, 1980). Carnivore-inflicted damage (e.g. tooth pits, scores, furrows, digested bones: Sutcliffe, 1970; Binford, 1981;

Brain, 1981; Haynes, 1983a; Binford, 1987; Cruz-Uribe, 1991) and the presence of bone cylinders, in the case of hyaenas (Binford, 1981; Brain, 1981; Bunn, 1983; Hill, 1989; Cruz-Uribe, 1991; Pickering, 2002; Kuhn *et al*., 2010) constitute direct evidence for carnivore involvement in the bone assemblage. Based on their hunting strategies, ways of consuming their prey and diet, leopards and hyaenids tend to produce specific and distinguishable skeletal element preservation patterns (Simons, 1966; Pickering, 2001a, 2001b; Carlson and Pickering, 2003; Pickering and Carlson, 2004; Pickering *et al*., 2004b), as well as different mortality profiles. Hence, leopards, practising an ambush type of predation, tend to be less selective in their prey and produce a catastrophic profile, with individuals of all age categories present. On the other hand, hyaenas tend to select the weakest individuals (the young and old) (Kruuk, 1972; Stiner, 1990; Cruz-Uribe, 1991; Pickering, 2002; Kuhn *et al*. 2010), and accordingly produce an attritional mortality profile (Domínguez-Rodrigo and Pickering, 2010). The abundance of small carnivores in the faunal spectrum (e.g. viverrids, herpestids and small canids) is often associated with bone accumulation by the brown hyaena, *Parahyaena brunnea* (Brain, 1980, 1981; Cruz-Uribe, 1991; Skinner and van Aarde, 1991; de Ruiter *et al*., 2009), reflecting the wide range in diet of this species (Skinner and Chimimba, 2005).

Finally, the occurrence of coprolites and digested bones constitute good evidence of cave occupation by hyaenids (Sutcliffe, 1970; Klein and Cruz-Uribe, 1984; Cruz-Uribe, 1991; Pickering, 2002; Berger *et al*., 2003; Lacruz and Maude, 2005; Kuhn *et al*., 2010), while the presence of juvenile carnivore remains, such as deciduous teeth, can indicate the use of the cave as a breeding lair (Lacruz and Maude, 2005; Kuhn *et al*., 2010).

Carnivore-collected assemblages and cave use by carnivores: the fossil evidence

Several extant and extinct species of carnivores to be known or suspected as potential bone accumulating agents in caves, namely *Parahyaena brunnea*, the brown hyaena, *Panthera pardus*, the leopard, and *Dinofelis barlowi*, an extinct species of false sabre-tooth cat, are present in the fossil assemblage (Dirks *et al*., 2010; Kuhn *et al*., 2011).

Various characteristics observed in the faunal assemblage are consistent with the occupation of a part of the cave by the brown hyaena, as well as some participation by this carnivore in the bone accumulation process. Only one carnivore coprolite has been prepared so far (Bamford *et al*., 2011), but another two potential coprolites have been identified during virtual exploration of blocks of calcified sediment. At Malapa, 23 bone cylinders have been recorded in the assemblage, suggesting the potential participation by hyaenids in the bone accumulation process. Small carnivores are well represented in the faunal spectrum (MNI of 5, including two herpestids, two viverrids and one small canid). Furthermore, the presence in the assemblage of two deciduous teeth attributed to *P. brunnea* (Kuhn *et al.*, 2011) seems to favour the hypothesis of the Malapa cave having been used as a den by this carnivore.

On the other hand, definite carnivore tooth marks are very rare in the assemblage and no digested bone has been recorded. The body part representation for hominins and bovids do not show any evidence of selection due to carnivore consumption (i.e. different from hyaenid and leopard refuse and scat assemblages; Carlson and Pickering, 2003; Pickering and Carlson, 2004). The significant number of partial skeletons, articulated elements and near complete individuals in the assemblage, such as MH1, MH2, and others, are not in accordance with an exclusively carnivore-accumulated scenario.

Consequently, two alternative hypotheses need to be considered. Firstly, based on the lines of evidence mentioned above, brown hyaenas could have occupied and used the cave as a breeding lair, and contributed to the accumulation of some bones, but only in the upper part of the cave system, which was accessible from the surface. Alternatively, the brown hyaenas were themselves victims of a fall into a vertical shaft, where they defecated and died. The deciduous brown hyaena teeth in the assemblage are not associated with any other juvenile skeletal remains, indicating that this individual lost its milk teeth in the cave, but did not die there, a scenario consistent with the breeding lair hypothesis.

### *1.2.2. Natural death trap scenario*

Bone accumulation through a pit-fall: theoretical model

The characteristics of a faunal assemblage, in terms of taxonomic composition, mortality profile, body part representation, and bone damage, are conditioned by the agent(s) and mode(s) of bone accumulation. Hence, several palaeontological and taphonomic features of a fossil assemblage can indicate it was accumulated through a natural pitfall, or death trap. Here, I propose the natural death trap scenario in its wider sense (*sensu* Pickering *et al*., 2004a), whereby animals either fall directly from the surface through a natural opening into a vertical shaft, or die accidentally inside the cave because they climbed down but are unable to exit. The latter applies especially to species with good climbing proclivities, such as carnivores and primates, which can venture inside caves, lose their way, and fall into vertical shafts because of a lack of light, or are unable to climb out, and eventually die inside the cave. This should be reflected in a fossil faunal assemblage dominated by primates and carnivores, as well as by the abundance of juveniles, which are more likely to be trapped (Cooke, 1991; Pickering *et al*., 2004a; Val *et al*., submitted).

Other indicators, such as the presence of antimeric sets of bones, complete or near complete bones, partial skeletons and/or articulated specimens, and a good representation of all skeletal parts, are classically associated with faunal assemblages accumulated via a natural death trap scenario (Costamagno, 1999b; Kos, 2003a, 2003b; Pickering *et al*., 2004a; Clarke, 2007; Coumont, 2009).

Bone accumulation through a pit-fall: the fossil evidence

The Malapa faunal assemblage exhibits several features that are characteristic of bone accumulation via a natural death trap scenario. A significant number of articulated elements and partial skeletons, including two hominins (MH1 and MH2) and other animals (bovids, carnivores and rodents), have been recovered. At least twelve antimeric sets of

bones of bovids, leporids and felids are present (see Appendix 6 for the complete list). Complete and near complete bones represent an important percentage of the assemblage. Carnivore bitemarks are very rare, with only 0.2% of the faunal assemblage exhibiting definitive chewing damage caused by a mammalian carnivore.

The skeletal part representation for the whole assemblage shows general good preservation of most of the elements, and a direct correlation between survivorship and bone density. There is no indication of a particular selection of elements by a factor other than differential conservation associated with bone density (e.g. no fluvial sorting, no selection by a carnivore). The hominins preserve most bones. Even when only considering the fragmentary individuals (MH3, MH4, MH5 and MH6) and the remains not attributed to any specific individual (MH), most skeletal parts are represented, such as elements of the cranium, long bones, pelvis, metapodials and phalanges. Only very fragile elements, such as the vertebrae and the ribs are absent. The non-hominin assemblage shows a density-mediated preservation pattern, where compact and dense elements are better preserved than spongy and fragile bones.

In summary, a natural death trap scenario is proposed, for at least some of the animals comprising the faunal assemblage, based on the presence of articulated and/or partial skeletons, antimeric sets of bones, density-mediated skeletal part preservation pattern, and low impact of carnivore damage on the bones. Based on the number of partial skeletons, antimeric sets of bones and articulated elements, it is possible to estimate that a minimum number of seven individuals, including the *Au. sediba* individuals MH1 and MH2, three bovids, one rabbit, and one small carnivore (see Appendix 6) were victims of the death trap.

Description of the type of death trap

The overrepresentation of carnivores and hominins, in other words of animals with good climbing abilities, could indicate the following death trap scenario: carnivores and primates enter the cave for various reasons (e.g. attraction to water or carrion, and in the case of primates, protection from carnivores). Some less agile individuals cannot find their way out, venture too far and/or fall down a vertical shaft deeper in the cave system, where there is little or no light. The complete absence of small monkeys, such as the extinct Colobine *Cercopithecoides williamsi*, whose remains are usually recovered in cave deposits in the Cradle of Humankind (Sterkfontein Member 2, Member 4, Member 5 StW 53 Breccia, Jacovec Cavern; Swartkrans Member 1 Lower Bank and Member 2, Kromdraai B, Cooper's D: Brain, 1981; Watson, 1993; Pickering, 1999; de Ruiter, 2003; Pickering *et al*., 2004a; Kibii, 2007), could suggest the existence of a way out of the cave for small animals skilled in climbing. The presence of large bovids (*Tragelaphus* sp.) amongst the animals considered as having accumulated through the death trap scenario implies the existence of a large shaft opening to the surface. I propose a combination of these two scenarios, whereby one or several opening(s) led to a vertical shaft collecting animals, skeletons, bones, stones and surface debris at the bottom in the form of a talus cone (primary deposit). This represents a gradual accumulation process, which can span long periods of time.

### *1.2.3. Contribution to the fossil assemblage by other biotic and abiotic agents*

Hominins

There is no evidence of hominin occupation of the cave, or hominin contribution to the accumulation of bones inside, in the form of burnt bones or butchery-marked pieces. A few stone tools have been recovered *ex situ* at the site and are currently being studied. Their contemporaneity with the faunal assemblage and/or their association with the *Au. sediba* fossils are the subject of ongoing investigations.

Other biotic agents

No other biotic agents, apart from carnivores and invertebrates, have played a major role in the formation of the faunal assemblage. Indications of porcupine presence are extremely scarce, in the form of two quills (Backwell *et al*., in prep.), suggesting that they did not make regular use of the cave. There is no direct evidence for any contribution by a bird of prey. The occurrence of microfaunal remains in the assemblage could be an indication of regurgitation pellets of owls nesting at the entrance of the cave. However, no digested microfaunal remains have been observed. The microfaunal assemblage could also represent individuals that died inside the cave from natural causes.

Gravity and rainfall

In the context of bone accumulation through a death trap, it is likely that some remains would have been brought inside the cave by abiotic agents, such as flowing rain water and gravity. This could, for instance, explain the presence of some highly weathered and fragmentary specimens, which were likely washed in from the surface, including the remains of large ungulates (giraffid/elephantid), unlikely to have entered the cave as complete animals/skeletons, given their fragmentary nature, poor preservation and lack of articulation. Large body size may also have prevented them from entering the cave through the shaft opening. Finally, some of the specimens showing trample marks could also have been introduced inside the cave by gravity; the trampling could have taken place outside the cave, on the surface.

## 1.3. Resedimentation to a lower part of the cave system by a debris flow: what is the evidence?

### *1.3.1. Geological evidence*

Several characteristics of the fossil-bearing geological Facies D, E and F indicate the action of a debris flow, as well as the deposition of sediments in an aqueous environment.

Facies D and E are composed of water-laid sediments made of sandstone, and contain abundant peloids, which show evidence of mechanical reworking in a water-logged context (Dirks *et al*., 2010). Facies E, which overlies Facies D, the geological unit containing the well-preserved hominin remains (MH1 and MH2 bones), shows a fining upward and preserves northwest dipping laminations indicative of directional water flow (Dirks *et al*., 2010). The presence of isopachous sparite in these two facies is indicative of rapid cementation taking place soon after the deposition of the sediments, in a phreatic environment. Facies D contains allochtonous material, mixed with autochtonous cave sediment, suggesting that this unit deposited through the action of a debris flow carrying elements from outside the cave and mixing them with elements from inside (Dirks *et al*., 2010). Facies E, on the other hand, is mostly composed of autochtonous sediment. This implies that after the debris flow occurred, the cave filled horizontally with sediments. Facies F, which is a grainstone deposit, also shows horizontal layering and graded bedding (Pickering *et al*., 2011).

### *1.3.2. Taphonomic evidence*

Bone surface modification

The experiment conducted by Hanson (1980) on cow bones transported in water, in a natural setting (East Fork River, Wyoming, USA), illustrates that long distance and/or long duration transport in water is required to produce visible abrasion and other transport-related damage on bones. For instance, some elements were transported in the river for nearly 2 kms without showing any trace of abrasion (Hanson, 1980). Shipman and Rose (1988) similarly concluded that grossly visible abrasion damage occurred extremely slowly on the mammal bones used in their experiment. The majority of the bones started showing macroscopic signs of abrasion after 35 hours inside the tumbling barrel, which according to the formula they propose, is consistent with transport in a river for about 25.2 km. Microscopic signs of abrasion occur more rapidly after a few hours (Shipman and Rose, 1988). At Malapa, clear abrasion damage (e.g. polish, abrasion, rounding) on bone

surfaces is very rare, whether at a gross or microscopic level, which excludes the possibility of transport in water over long distance and/or for a long period of time.

Skeletal element representation

The survivorship observed for the faunal assemblage is consistent with a density-mediated conservation pattern, where the denser bones are better represented than the more fragile ones. Comparisons with experimental results (Voorhies, 1969; Boaz and Behrensmeyer, 1976; Coard and Dennell, 1995; Coard, 1999) and studies of fossil assemblages (Behrensmeyer, 1975, 1988; Smith, 1980, 1993) concerning bone transport potential show no evidence of any kind of sorting by fluvial transport in the Malapa faunal assemblage. Elements from the lag group (e.g. mandible, isolated teeth, scapulae) are as well, if not better, represented as easily transportable elements (e.g. vertebrae, sacrum). However, there is no experimental data on bone transport in the context of a vertical water flow, all information comes from experiments conducted in horizontal recirculating flumes (Voorhies, 1969; Boaz and Behrensmeyer, 1976; Coard and Dennell, 1995; Coard, 1999; see Chapter 2).

Spatial distribution of the bones

Data about bone orientation, derived from experimentally created water current, show that the long bones tend to orientate themselves parallel to the flow, especially when the bones are submerged (Voorhies, 1966; Boaz and Behrensmeyer, 1976; Coard and Dennell, 1995; Coard, 1999). On the other hand, in the case of bones floating in shallow water, it has been observed that they tend to orientate perpendicular to the current. Finally, experimental data show that articulated elements always travel faster than disarticulated elements, and have a higher transport potential (Coard and Dennell, 1995). At Malapa, there is no definitive pattern of orientation for the long bones. The long bones of MH2, recovered in the “arm block”, follow a south-north direction, while the hypothetical 3D reconstruction indicates that MH1 is lying horizontally, with a general

northeast-southwest orientation for the long bones (right ulna, humerus and clavicle, and left femur). Movement from multiple directions has affected the remains of MH2 and MH; from north to south and from east to west for MH2, and from east to west and west to east for MH1. Marked displacement is observed in the rotation and reversed position of some of MH2 elements, such as in the displaced the manubrium and the first two right ribs.

### *1.3.3. Single chamber versus several chambers?*

Input from different parts of the cave system

There is taphonomic evidence for multiple origins for the fossils comprising the faunal assemblage (see above). The bones, bone fragments, skeletons, rocks, and sediments accumulated in the final deposit at the bottom of the cave system come from different chambers and parts of the cave. A mixing of faunal assemblages is the most logical explanation for the two very different modes of accumulation occurring in one deposit: through a natural death trap, in a part of the cave system without access to scavengers on one hand, and through the contribution of brown hyaenas using the Malapa cave as a breeding den on the other. The porcupine quills could also come from the hyaena den as these two taxa commonly alternate occupation. Carcasses decomposing on the talus cone beneath the death trap would attract scavengers. At Malapa, there is no evidence of carnivore damage on the skeletons, which have accumulated via the death trap, indicating that this part of the cave offered no access by mammalian scavengers to the carcasses. It does not make sense that this same part of the cave would at times be accessed by the brown hyaenas and used as a den. It is rather an indication of the existence of two different cave chambers, whose bone assemblages were mixed, possibly through the action of a debris flow and/or other agent(s), and buried at the bottom of the cave.

Were MH1 and MH2 moved from where they fell?

Dirks and colleagues (2010) proposed that the hominins and other animals fell through a vertical shaft into an upper chamber of the cave. They accumulated as part of a talus cone before being transported *en masse* by a debris flow to a lower chamber, where burial, decomposition and fossilisation took place. I propose an alternative interpretation, with only one chamber, located at the bottom of the death trap, in a lower part of the cave system. Hominins and associated animals died and decomposed where they fell on the talus cone. A debris flow did not transport them any great distance, it only caused some dispersion and movement inside the lower chamber; floatation could also have occurred. I refer to "primary" and "secondary" deposits, which does not imply any difference in space, but only a difference in time, rather than to "upper" and "lower" chambers. The primary deposit refers to the bottom of the talus cone, underneath the vertical shaft, where the hominins and other animals fell and started to decompose, before they were buried. The secondary deposit refers to the bottom of the cave, possibly to a pool, and where the carcasses were buried and fossilized.

### *1.3.4. Discussion: problems encountered with the debris flow hypothesis*

Several elements indicate that the faunal assemblage underwent some mixing. Firstly, there are contradictory taphonomic signals, such as evidence for cave occupation by brown hyaena on the one hand, and accumulation via natural death trap scenario with no contribution by carnivores on the other. Secondly, the assemblage is characterised by an extreme heterogeneity of the fossils in terms of preservation, especially visible when comparing material recovered from calcified sediment with material from decalcified sediment. Finally, Facies D is composed of mixed allocthonous and autochthonous sediments. However, whether a debris flow is the agent responsible for the mixing is difficult to determine, as the results of bone surface modifications and spatial analyses are not in accordance with a debris flow scenario. The absence of polished and abraded bones in the assemblage, as well as the state of articulation of numerous faunal remains indicate

that, if some transport of material occurred, it was only for a very short distance. There is no clear orientation pattern or preferential direction for the elongated bones inside the deposit. For instance, MH1 and MH2 skeletons do not follow the same orientation, as illustrated by the virtual reconstruction; they are almost perpendicular to each other. The movement that affected MH1 and MH2 was from various directions (east to west and west to east for MH1; south to north, east to west and rotation for MH2). If the hominin skeletons, together with other faunal remains, were already in a lower chamber when the debris flow occurred, an absence of specific orientation pattern could be possible. The action of the debris flow would cause *movement* of the bones and skeletons but not necessarily *transportation*. Depending upon the density and content of the debris flow, floatation and dispersion inside the pool of water could be expected. If a debris flow occurred and created a pool of water at the bottom of the cave system, the pool would have been of relatively small size, as shown by the very limited dispersion of the hominin remains (MH1 and MH2) in the deposit. If MH1, which is disarticulated, was affected by debris flow, even only through floatation, his remains should be more scattered across the deposit, which is not the case (see for instance the position of the *in situ* teeth just above the skull). Finally, the burial position of MH1 and MH2 is not consistent with the position of bodies floating on the surface of a pool of water (see below 2.4 and 3.3. Final burial position). This suggests that they did not decompose in a pool of water, either because they decomposed in a dry cave chamber before being transported by debris flow, while already skeletonised and partially mummified, or because there was no debris flow and no pool of water.

To conclude, whether the debris flow has played a major contribution to the mixing of the faunal assemblage remains to be confirmed. It is worth considering the possibility that other post-depositional agent(s) have caused the displacement of the bones in the deposit, for instance insects reworking the sediments, as suggested by the presence of abundant insect damage mostly on the decalcified material. This will be further investigated in the future.

Figures 8.1 to 8.3 illustrate the taphonomic scenarios proposed previously and here for the Malapa faunal assemblage, including the entry of the bodies, bones and other remains inside the cave system (Figure 8.1), the hypothetical “debris-flow event” (Figure 8.2) and the current morphology of the deposits, after erosion (Figure 8.3). The two possible hypotheses concerning the location of the primary deposit inside the cave (in the upper versus lower chamber) are represented.

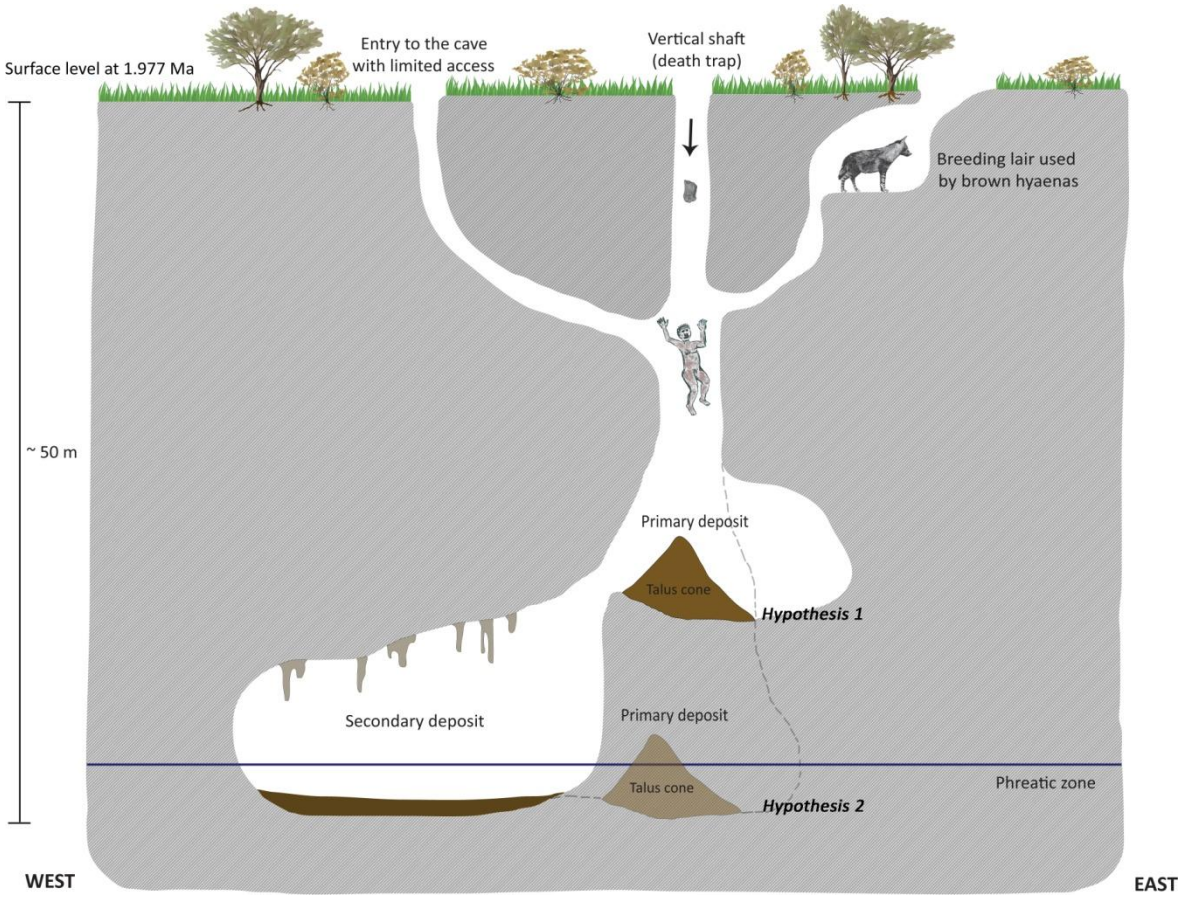



**Figure 8.1**. Stage 1: bone accumulation in the primary deposits (den occupied by the brown hyaena, and talus cone at the bottom of the vertical death trap). View from the south.

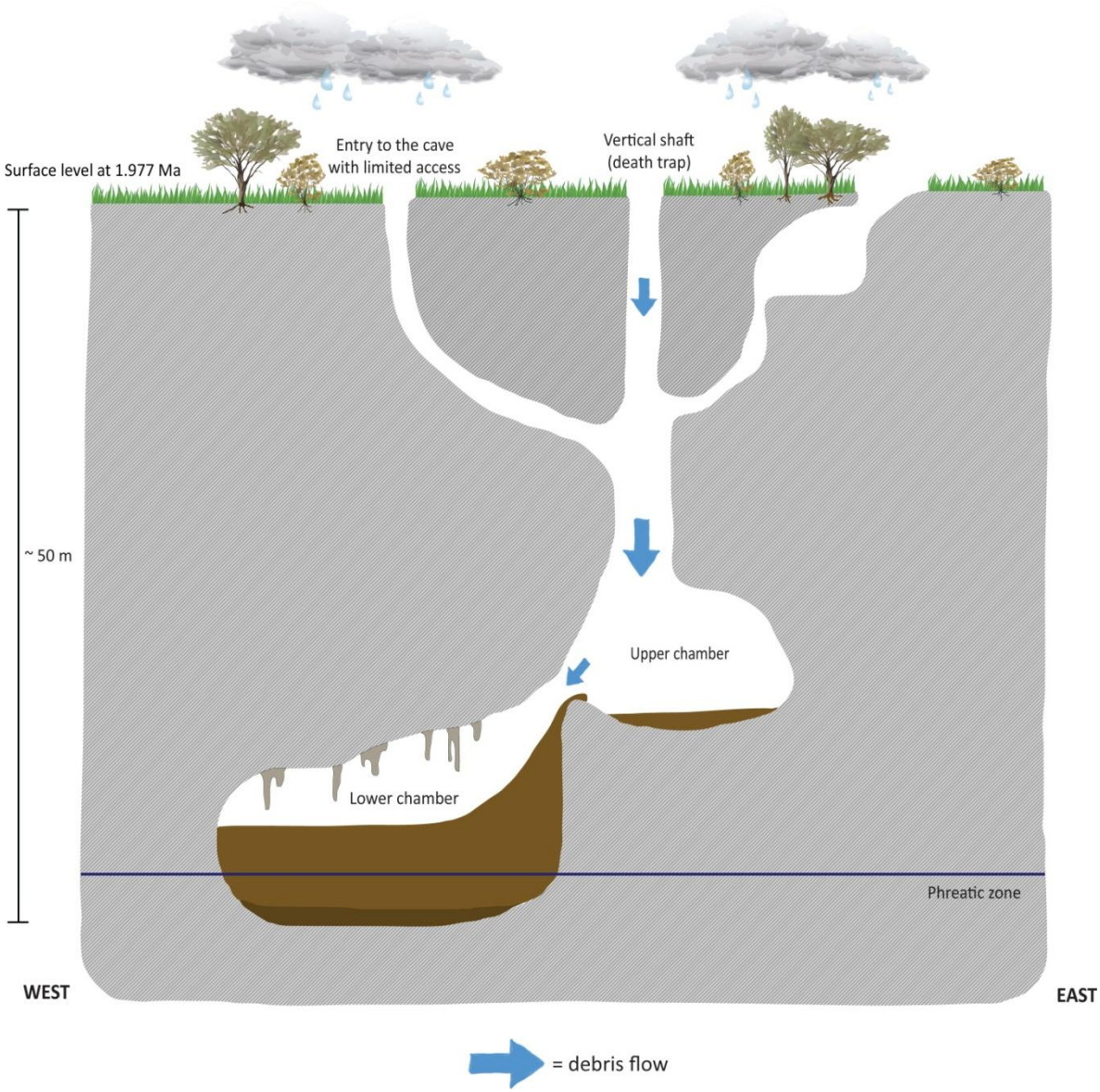



**Figure 8.2**. Stage 2: primary bone accumulations are transported by the debris flow to the secondary deposit. View from the south.

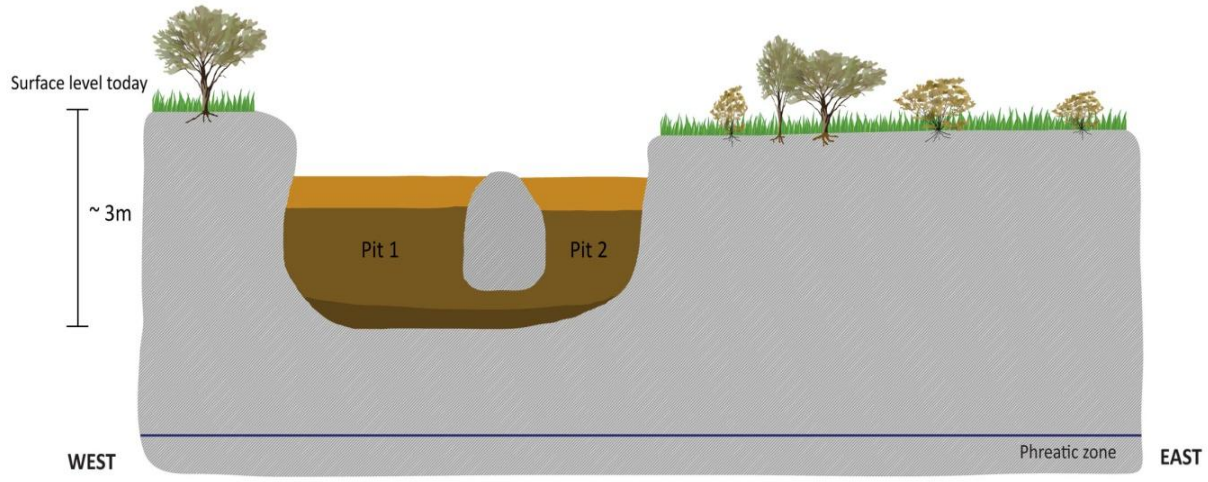



**Figure 8.3.** Stage 3: present state of the deposits, after erosion of the upper part of the cave system. View from the south (the lighter brown layer, on top of the sequence, is consistent with Facies F, which deposited after the debris flow event).

The following section presents a hypothetical reconstruction of the different steps that have led to the preservation of the hominin remains, from their entry into the cave system until their burial and fossilisation inside the deposit. The case of MH2, which is the best preserved individual, is described first, followed by MH1 and the other individuals.

## 2. TAPHONOMY OF THE ADULT FEMALE MH2

### 2.1. Mode of accumulation in the deposit

It has already been demonstrated (see above) that MH2 exhibits features associated with an accumulation via a vertical shaft that opened to surface and became a natural death trap (near-complete skeleton, numerous complete bones and elements in articulation, absence of carnivore damage), which had a connection to a part of the cave inaccessible to carnivores and rodents. The MH2 carcass remained for some time where it landed after falling onto the talus cone, in the primary deposit before being buried inside sediments in the secondary deposit (Facies D), either after mass flow transportation at the bottom of the cave by a debris/mud flow, or after normal continual accumulation of talus cone sediments.

## 2.2. Time of exposure and state of decomposition before burial

One of the main questions to be answered concerns the duration of exposure of the carcass before burial – and consequently the state of decay when burial occurred. Understanding the duration of exposure of MH2 has various implications, in terms of explaining the general preservation of the remains, as well as indicating whether or not soft tissue, such as skin, was still present at the time of the burial. Different aspects of the bones can help estimating the time of exposure in the primary deposit, namely the weathering stage(s) of the bones, the pattern of disarticulation of the skeleton, and insect damage present on the bone surface.

### *2.2.1. Decomposition rate: the theory*

Under temperate conditions, the decomposition processes (see Table 8.1), including autolysis, putrefaction, and adipocere formation (also called saponification) or natural mummification (e.g. Weigelt, 1989; Clark *et al*., 1997; Vass, 2001; Duday, 2009; Gennard, 2012), take place in a matter of days or months for bodies exposed on the surface (Clark *et al*., 1997) and up to 15 to 25 years for bodies that are buried in soil (e.g. in graveyards or peat bogs; Fiedler and Graw, 2003). To calculate the time required for a body placed on the surface to be completely decomposed, in other words to reach the dry stage, Vass *et al*. (1992) proposed a simple formula, whereby the duration of decomposition of soft tissue is related to the temperature in which the body is decaying. Hence, the number of days needed for the body to become skeletonised (y) equals 1285 divided by the average temperature (x) or y = 1285/x.

**Table 8.1**. Decomposition stages for human cadavers (from Vass, 2001 and Duday, 2009).

| STAGE | DESCRIPTION |
|---|---|
| FRESH | Beginning of decay: autolysis of the cells; *rigor mortis*; body temperature acclimating with the ambient temperature, and discolouration of the skin. |
| BLOATED | Active putrefaction due to the action of microorganisms, such as fungi and bacteria, which cause the destruction of soft tissues, turning them into gases, liquids and molecules. The putrefaction is associated with anaerobic fermentation and results in the distension of tissues (the abdomen can burst if the temperature is high enough) and a greenish coloration of the skin. |
| ACTIVE DECAY | Saponification or adipocere formation (hydrolysis of fat which can lead to the formation of soap) resulting in the formation of creamy, yellowish and wax-like substance on the body. |
| ADVANCED DECAY | Drying out of the soft tissue; the cadaver is flat. |
| DRY | Desiccation: only hair, dried out skin, tendons and bones remain; the bones are exposed and undergo diagenesis, whereby the organic components are replaced by inorganic components. |

Various factors have a combined influence on the decomposition rate, such as climatic and environmental conditions (e.g. level of humidity, temperature, and season), location of the body (in the shade versus directly exposed to sunlight or on the surface versus buried or in water), impact of scavengers, and state of the corpse (e.g. diseased versus healthy person, presence or absence of wounds). Hence, the decay of bodies placed in the shade tends to be slower than for bodies exposed to the sun light and heat (Shean *et al*., 1993; Dillon, 1997; MacGregor, 1999a, 1999b: in Anderson, 2010; Sharanowski *et al*., 2008; Prado e Castro *et al*., 2011). Different seasons are associated with variations in temperature, sunlight and insect abundance, which have an impact on the rate of carrion decomposition. The decay tends to be quicker during the warmer months of the year, which are consistent with maximum heat and sunlight (MacGregor, 1999a, 1999b: in Anderson, 2010), as high temperatures are usually conducive to fast decomposition (Feidler and Graw, 2003). The composition and abundance of the insect assemblage found on a corpse vary from one season to the next, also influencing the rate of decomposition, with the colder months usually being characterised by less abundant

insects (Sharanowski *et al*., 2008; Kelly *et al*., 2009). Disruption and feeding off the carcass by scavengers, such as mammalian carnivores and rodents, greatly speed the decay process (Ellison, 1990; Mann *et al*., 1990; Dillon, 1997). Scavengers remove large quantities of flesh, skin, and viscera from the body, accelerating the putrefaction process. By exposing large areas of decaying tissues, they also create favourable conditions for insects that colonise the carcass in early stages, for instance by creating wounds where blow flies can lay their eggs (Ellison, 1990; Dillon, 1997; Turner and Wiltshire, 1999). Buried bodies, protected from elements that hasten the decomposition process, such as exposition to scavengers, insects, and temperature variations, take longer to decay than bodies exposed on the surface (Mann *et al*., 1990; Fiedler and Graw, 2003; Simmons *et al*., 2010a, 2010b). Complete decomposition of a body in earth can take between 15 and 25 years, contra the few months necessary for a body on the surface to reach skeletonization (Clark *et al*., 1997; Fiedler and Graw, 2003). Bodies placed in water also take longer to decompose, especially due to the limited (but existing) action of insects (Payne and King, 1972; Haefner *et al*., 2004; O'Brien and Kuehner, 2007). A generally accepted postulate (i.e. the Casper's dictum) is that one week of decomposition for a body on the surface equals 2 weeks for a body in water and 6 to 8 weeks for a body buried in the soil (Fiedler and Graw, 2003). The post-mortem changes take place faster on individuals with wounds or that died because of bacterial or viral infections; on the other hand, individuals whose death is connected to the ingestion of antibiotics, poisons and drugs, undergo slower decomposition (Janaway, 1987; Willey and Heilmann, 1987: in Fiedler and Graw, 2003; Mann *et al*., 1990).

### *2.2.2. Indications from the fossils*

Weathering stage

All MH2 remains show weathering stage 1 or 2 (*sensu* Behrensmeyer, 1978), with superficial or slightly deeper cracks on their surfaces. This is indicative of some time of

exposure before burial. Experimental data about weathering in an open environment demonstrate that it takes between 0 and 3 years for the bones to reach stage 1 (Behrensmeyer, 1978), while in a tropical rain forest, it can take up to 10-15 years (Tappen, 1994). Miller (1975) observed that small superficial cracks can start appearing shortly after the bones become exposed and, in some cases, even before the periosteum has been completely removed. In any case, cracks on bones only appear once the soft tissue has been removed and the bone surface is exposed (Miller, 1975; Behrensmeyer, 1978). The fact that the MH2 skeleton was located in a cave means that is was protected from elements responsible for weathering, such as direct sun, extreme temperature variations and moisture fluctuations (Behrensmeyer, 1978; Lyman and Fox, 1989). In sub-aerial context, weathering does not stop, but is inhibited (Miller, 1975; Behrensmeyer, 1978; Potts, 1986; Shipman, 1981a; Todd and Frison, 1986). This confirms that the body of MH2 remained for at least several months and possibly a few years before being buried.

State of articulation

In human skeletons exposed on a dry surface, only a few weeks are necessary for the unstable joints to disarticulate, while several years are required for the persistent joints to disarticulate (Duday *et al*., 1990; Maureille and Sellier, 1996; Duday, 2009). Observations on desiccated carcasses of East African mammals exposed on the surface show that disarticulation is almost always complete after five years (Hill and Behrensmeyer, 1984). MH2 preserves most elements in articulation or anatomical proximities, including persistent and fragile articulations. Weathering stages 1 and 2 on the MH2 bones suggest that the body remained exposed for at least a couple of years, in the primary deposit, which is longer than the time required for all fragile articulations to dislocate. The fossil evidence shows the preservation of articulated elements and anatomical proximities, including unstable articulations, in the secondary deposit. This suggests that another taphonomic process, namely desiccation, must have affected the carcass in the primary deposit, preserving the articulation of the skeleton prior to burial,

especially during short distance transportation by a debris flow (see below 2.3. Evidence for natural mummification).

Insect damage

The decay of a body is accompanied by colonisation of the carrion by insects. Various species of insects, mostly from the Orders Diptera and Coleoptera, are found successively on the carcass as it decomposes. Some are necrophagous, feeding directly off the fresh organic matter (e.g. Calliphoridae, Sarcophagidae and Silphidae), while others are predatory, feeding on the former (e.g. Staphylinidae and Histeridae). Usually, the first wave of insects is composed of blow flies and carrion flies (Calliphoridae and Sarcophagidae), attracted by the odour of the carcass, which arrive during the first stage of decomposition, the fresh stage. The adults lay eggs on the carcass, which become larvae or maggots. Significant masses of maggots are found on the carrion during the following stages of decomposition, the bloated and active decay stages. During these stages, the fly maggots attract other insects, especially predatory beetles (Staphylinidae and Histeridae, followed by Dermestidae). The last two stages of decomposition, advanced decay and dry stages, see a last wave of insects colonising the carcass, attracted by the remaining dry matter, such as hair, skin and tendons (e.g. Cleridae, Dermestidae, Scarabaeidae, and Trogidae) (Mégnin, 1984; Smith, 1986; Weigelt, 1989; Ellison, 1990; Byrd and Castner, 2010). Table 8.2 provides a list of species of insects mentioned in the text, with their common name.

**Table 8.2.** Species of insects found on carcasses and mentioned in the text.

| ORDER | FAMILIES |
|---|---|
| DIPTERA | Calliphoridae (blow flies/carrion flies) |
| | Sarcophagidae (flesh flies) |
| COLEOPTERA | Scarabaeidae (scarab/scarab beetles) |
| | Histeridae (Clown beetles/Hister beetles) |
| | Staphylinidae (rove beetles) |
| | Cleridae (checkered beetles) |
| | Dermestidae (dermestid beetles) |
| | Silphidae (large carrion beetles/carrion beetles) |
| | Trogidae (hide beetles) |

The only MH2 fossil showing insect damage is a fragment of fibula shaft (specimen UW88-84), which was recovered from *ex situ* calcified sediment. The traces are located below the manganese, which indicates that they are ancient, most likely pre-burial, made during decomposition of the carcass. The presence of the marks on the bone surface suggests that the bones were exposed and accessible to the insects that produce them. This means that these insects must have accessed the carcass at a late stage of decomposition, most likely during the advanced decay stage or the dry stage, and were feeding on the remaining dry matter (skin, hair, tendons, and possibly even bones). The best match for some of the marks with the actualistic data is with damage produced by hide beetles (Trogidae, *Omorgus squalidus*). Adult hide beetles are late colonisers, and usually arrive on a carcass at the end of the bloating stage; they mate and feed on moist tissues, while the larvae, which feed on dry matter, complete their development during the dry stage, when only dried out skin, tendons, hair, and bones remain (Smith, 1986; Archer and Edgar, 1998; von Hoermann *et al*., 2012). Hide beetles are not known to feed on bones, which suggests that the necrophagous larvae incidentally produced the traces on the Malapa hominin remains, while feeding on the dry skin covering the skeleton. The morphology of the damage is consistent with feeding rather than pupating activities. Ongoing research on the mouth parts of various invertebrates, including hide beetles and their larvae, will help identify the modifier of the bones. Only one fragment of MH2 was affected, which seems to support that the insects were feeding on the dry matter rather

than on the bones. If the insects were feeding on the bones, they would have left far more abundant marks, especially if one considers that the modifications are pre-burial, at a stage where the skeleton of MH2 was still articulated. The impact of scavengers on a carcass is said to be directly linked with the impact of insects; when scavengers feed on a carcass they can remove large quantities of organic matter (muscles, viscera, skin), which means that there is not much left for the insects that colonise later (Ellison, 1990; Dillon, 1993). It seems likely that the opposite is true: if the carcass is not disturbed by scavengers, as it is the case for MH2, significant amount of skin and other soft tissue should remain at the end of the decay process, during the dry stage, making the carcass attractive to the late colonisers, such as hide beetles.

Summary

The presence of cracks due to weathering on all specimens, as well as the occurrence of insect damage, some of which may have been produced by a species of late coloniser, indicate that MH2 had reached skeletonisation when burial took place. The bones were exposed to weathering, and insects could feed on the remaining dry matter, leaving traces on the bones. An estimation of the exact length of time taken for the decomposition process of MH2 is difficult. However, an estimation of the *minimum* length of time required for the carcass to reach the dry stage is conceivable, by using the formula proposed by Vass *et al*. (1992; see above), based on the ambient temperature and by taking into account the external and internal conditions surrounding the decomposition that have an impact on the timing of decay. Today, the temperature inside dolomitic caves in southern Africa is constant (between 17.1 to 18.6 C°: Barrett *et al*., 2004). If the temperature was the same 2 million years ago, it would have taken at least between 71.4 (1285/17.1 C°) and 69.1 (1285/18.6 C°) days, just over two months, for the body of MH2 to decay and become skeletonized. The average temperate in the Sterkfontein Valley between 2 and 1.5 Ma is thought to have been higher than today by a few degrees (Brain, 1995; Avery, 2001). Even with an increase of temperature of 5 degrees inside caves

around 2 Million years ago, the decomposition would have taken a minimum of 1285/23 C° = 55.8 days, or just under two months. At that stage, only bones and dry matter (skin, tendons and hair) would remain. The type of environment in which the decay of MH2 took place in a deep underground cave chamber is associated with external conditions that tend to slow down the decomposition process, where the carcass is away from sunlight and heat, there are negligible fluctuation in temperature inside the cave, no disruption of the carcass by scavengers, and limited attraction from insects. These factors would have possibly added some days, weeks or even months to the minimum number of 55.8 days calculated, based on temperature only.

## 2.3. Evidence for natural mummification

### *2.3.1. Mummification process: definition and required conditions*

Natural mummification is the survival of soft tissue, such as skin and ligaments, on a skeleton, taking place during the decomposition process; it is associated with the dehydration or desiccation of soft tissue (Vass, 2001). Various external (e.g. temperature, humidity, aerobic versus anaerobic environment: Vass, 2001; Murphy *et al*., 2003; Duday, 2009) and internal conditions (e.g. conditions of the body at the time of death: Amendt *et al*., 2004) can lead to mummification. Hence, a very low humidity level, combined with windy conditions, observed in dry environments such as deserts and arctic regions (Weigelt, 1989; Maureille and Sellier, 1996; Vass, 2001), or in closed rooms kept hot, dry and windy (Jit *et al*., 2001; Campobasso *et al*., 2009; Introna *et al*., 2009), can be conducive to natural mummification. Underground and enclosed contexts, such as caves, with combined stable conditions of temperature and humidity, can also lead to natural mummification (Esterhuysen *et al*., 2009). The nature of the soil on which the body is lying has an influence on potential mummification. Clay-rich soils have been shown to slow down the decomposition process (Turner and Wiltshire, 1999; Introna *et al*., 2009), quickly absorbing the fluids liberated by the body during decomposition, and halting the putrefaction process, enabling mummification to take place (Introna *et al*., 2009). The

presence of lime in the ground can also stop the decomposition process and permit mummification. This has for instance been observed in medieval Korean bodies preserved in coffins surrounded by a lime-soil mixture, which is considered to be one of the main factors leading to natural mummification and preservation of these bodies (Shin *et al*., 2003, 2008; Kim *et al*., 2008). Observations conducted by Mann *et al*. (1990) on decomposition showed that human bodies placed on concrete decompose slower and mummify faster than bodies placed directly on natural ground. Finally, a recent experiment on the decomposition rate of pig carrion in different types of soil illustrates the role of quicklime CaO and hydrated lime $Ca(OH)_2$ in dramatically slowing down the decay of the carcasses (Schotsmans *et al*., 2012).

### *2.3.2. Evidence of natural mummification in the fossil record*

In the fossil record, when the skin has disappeared, some characteristics can indicate that mummification took place prior to fossilisation. In particular, the preservation of fragile articulations, combined with the non-preservation of persistent articulations, or so-called *"dislocation en ordre paradoxal"*, dislocation in paradoxical order (Maureille and Sellier, 1996), is a good indication of mummification (Arbogast, 1995; Maureille and Sellier, 1996). It suggests that, while the persistent joints have disarticulated, the unstable joints, which generally consist of elements covered mostly by skin, such as the hands and feet, which are less subject to the putrefaction process (Arbogast, 1995), remain intact, and due to the desiccation of the skin that keeps the bones articulated.

### *2.3.3. Favourable conditions for natural mummification at Malapa*

The conditions of temperature, ventilation and humidity inside dolomitic caves can be conducive to mummification (Esterhuysen *et al*., 2009); the temperature is stable, while the humidity is relatively low (Barrett *et al*., 2004). Furthermore, the chamber at Malapa, where MH2 would have fallen through the death trap, most likely presented an

extremely difficult access, thus preventing carnivores, porcupines and others to disturb the decomposition and mummification processes. The presence of an opening to the surface, at the top of that cave chamber, would have allowed some ventilation, which is an important condition for desiccation. Finally, the dolomitic cave system, in which the Malapa hominins have been recovered, is characterised by the presence of limestone (i.e. calcium carbonate $CaCO_3$) in the rock (Dirks *et al*., 2010), which would have retarded decay and contributed to the mummification process. *In situ* remains of MH2 (inside the "arm block") were recovered directly in contact with the limestone-rich flowstone underlying Facies D.

### *2.3.4. The case of MH2: what is the evidence?*

The order of disarticulation observed for MH2 follows a logical order, where all the elements preserved in articulation are those with persistent joints, while the elements disarticulated and preserved in anatomical proximity are those with unstable joints (see Chapter 6, Table 6.2). Therefore, no dislocation in paradoxical order, associated with mummification, is observed. However, based on the evidence of a long time of exposure in the primary deposit (weathering stages 1 and 2), which is much longer than the time required for unstable articulations to dislocate (only a few weeks, Duday *et al*., 1990, Duday, 2009), I argue that if these bones were disarticulated, with no tissue to hold them together, they would have dispersed when disturbed by the debris flow or through other post-depositional processes. On the contrary, in the case of mummification, dry skin and ligaments around unstable joints, such as the thorax, hands and knees, would have held the bones together during movement, burial and diagenesis.

## 2.4. Final burial position

A hypothetical reconstruction of the burial position of the MH2 skeleton (e.g. position of the bones inside the deposit, displacement of skeletal elements from their anatomical position) is proposed here. Although all aspects of the following reconstruction

cannot be demonstrated with certainty, they are consistent with the fossil evidence observed, such as the position and orientation of the bones inside the "arm block". Whether burial was caused by a debris flow or normal sedimentation process is unclear.

The MH2 skeleton was still maintained in articulation by mummified skin when burial occurred. MH2 would have come to rest at the bottom of the lower chamber, on top of the flowstone, head first toward south, lying on her back, with the rest of the body following and pointing north, the upper limbs extended (as illustrated by the position of the arm and hand inside the arm block), and the lower limbs slightly flexed with the knees pointing east (Figure 8.4). The hypothetical reconstruction for MH2 position in the deposit indicates that she was lying horizontally, with the body generally oriented from south to north. One possibility is that the skull detached when the body hit the flowstone. In mummified bodies, the areas around the neck, the armpits and the groin are very fragile and can break easily because of significant shrinkage (Spitz and Fisher, 1980). This would mean that the skull either rolled below the body, in which case it is still embedded in the "arm block", or detached and floated to the surface, in case the burial took place in an aquatic environment. In this case, it would be in an isolated block of *ex situ* sediment removed from the upper part of Facies D and not yet prepared (see Chapter 9, Where are the missing remains?). The displacement of some bones in relation to their anatomical position occurred during and/or possibly after burial in a fluid environment (e.g. soft sandy sediments) still allowing for some movement. The legs were bent toward the left (i.e. western part of the deposit), with the left leg on top of the right leg, the knees pointing east and the ankles facing west. The arms were extended and not crossed, with the right arm orientated south-north, on the right side of the body, and the left arm orientated south-north as well, on the left side of the body (see Chapter 9, Where are the missing remains?). Some fragile parts might have disarticulated inside the unconsolidated sand, such as the articulation between the right femur and acetabulum, around the right elbow, and in the cervical and upper part of the thoracic cage. The lower limbs were displaced toward the upper limbs (i.e. towards the south of the deposit), the radius and

ulna towards the humerus, scapula and mandible and the right ribs towards the left. A north-south displacement – or upward movement of some bones towards the upper part of the body – has been observed for the radius and ulna for instance, which have been pushed toward the humerus and scapula, and for the clavicle, which has been pushed towards the mandible.

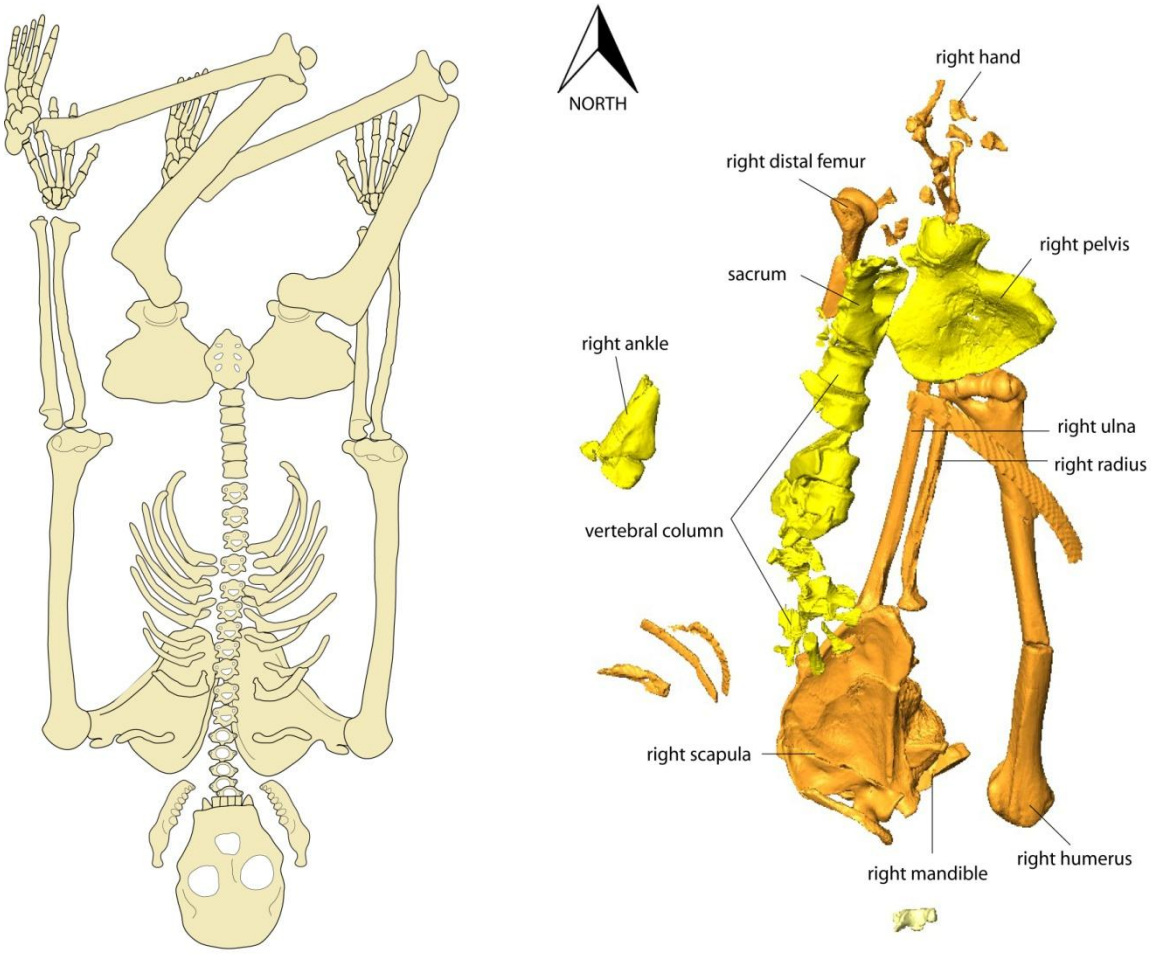



**Figure 8.4**. Burial position of MH2, viewed from the top (left: hypothetical burial position, before displacement and including the missing bones; right: burial position as recovered from the deposit, including only the bones that have been found).

The position of some bones is difficult to explain. This is especially the case for the first rib, the medium rib UW88-154, and the manubrium, which have rotated from their anatomical position and are located below the scapula. The decomposition of the organs

and tissues present in the thoracic cage creates a void inside the body. Whether the cadaver is buried in a void later filled by sediments or in an volume filled with sediments, the space created by the decomposition of the organs and the tissues present inside the thoracic cage usually lead to a flattening of the ribs, a dislocation of the sternum and sometimes the rotation of vertebral segments (Duday, 1990, 2009). It only very seldom happens that the space created is filled by sediments, thus maintaining the original thoracic volume (Duday, 1990). The preservation of the initial volume of the thoracic cage only happens in two cases: when the sediment gradually replaces the flesh, as it decomposes, or when the body is buried inside a gutter-shaped grave, in which case the ribs are supported by the sides of the narrow pit (Duday, 2009). All the MH2 ribs recovered, and for which a side has been attributed (UW88-58, 61, 143, 144, 145, 165, 166) are right ribs. They are all on the same level as the scapula, except in the case of the first rib. The movement of the ribs observed for MH2 can be partially explained by a natural phenomenon of rib cage flattening, and perhaps by floatation in water, if present, inside the bottom of the cave. However, floatation does not seem to explain the position of the first rib and manubrium located under the scapula. Another factor, yet to be identified, must have caused some post-depositional movement.

The hypothetical burial position of MH2, as reconstructed in Figure 8.4, is consistent with a natural posture, most likely close to the position in which the individual died, showing no hyper flexion, no *rigor mortis* and no trace of agony. It is not consistent with a belly up, head up or dorsal up position, which are positions usually associated with burial in an aquatic environment (e.g. Ochev, 1995; Haefner *et al*., 2004; O'Brien and Kuehner, 2007; Stanford *et al*., 2011; Fordyce *et al*., 2012). This suggests that MH2 did not decompose in a pool of water. Decomposition in water is associated with various stages of floating and sinking (O'Brien and Kuehner, 2007). Floating of the body leads to belly up, head up postures and sometimes dorsal up postures, with all the limbs relaxed and placed either horizontally or towards the bottom, especially if the body is dorsal up. This floating position is well documented in palaeontological (e.g. Ochev, 1995; Stanford *et al*., 2011;

Fordyce *et al*., 2012) as well as in forensic contexts (e.g. Haefner *et al*., 2004; O'Brien and Kuehner, 2007). Consequently, if there was a debris flow inside the Malapa cave system, it must have occurred after MH2 was skeletonised and mummified, and the position in which she died was maintained by dry skin and tendons. It could also point toward the absence of debris flow and associated pool of water at the bottom of the cave. In that case, MH2 would have decomposed on the ground in her death posture, mummified and been progressively covered and buried by soft sediments.

## 3. TAPHONOMY OF THE JUVENILE MALE MH1

### 3.1. Mode of accumulation in the deposit

Based on the same evidence as MH2 (e.g. near complete skeleton, abundant complete and near complete bones, absence of carnivore damage), it is proposed that MH1 entered the cave system in the same way as MH2, by accidentally falling through a vertical shaft that led to the primary deposit, where it formed part of a talus cone. Evidence of insect gnawing on the roots of the upper right incisor and canine of this individual suggest that these teeth detached from the skull, probably due post-depositional process rather than an impact, as is indicated by the absence of fracture of the maxilla and the fact that the teeth are complete. The body decayed in the primary deposit, possibly mummified, before being buried next to the skeleton of MH2 in the secondary deposit (Facies D).

### 3.2. Time of exposure and state of decomposition before burial

As for MH2, the weathering stage of the bones, the degree of articulation, and the type and location of insect damage on the skeleton can help estimating the duration of exposure of MH1 in the primary deposit.

### *3.2.1. Weathering*

MH1 remains exhibit evidence of weathering (i.e. stages 1 and 2) in the form of superficial and deeper cracks, indicative of a time of exposure of several years (Behrensmeyer, 1978; Tappen, 1994) in the primary deposit.

### *3.2.2. State of articulation*

MH1 does not preserve any element in articulation or anatomical proximity, which indicates that his body remained in the primary deposit long enough for his bones to disarticulate. This suggests either that MH1 was in a more advanced state of decay than MH2, or experienced a faster rate of disarticulation and dispersion due to his young age, with long bones still fusing and articulations still ossifying (see below for a discussion about the time of entry of MH1 and MH2). However, the 3D reconstruction shows very little dispersal for MH1 remains inside the deposit, which suggests that at least some elements of the body were still held together, in all likelihood through partial mummification, as for MH2.

### *3.2.3. Insect damage*

MH1 presents the same type of insect modifications as MH2, on four remains, including three with ancient damage below the manganese (a fragment of the left ischium and the upper right incisor and canine) and one with recent damage, on top of the manganese (left ilium). The same arguments as for MH2 can be proposed for the traces observed on the ischium: some of the damage was likely caused by hide beetles, at a stage when the carcass was dry, and indicates that MH1 had reached skeletonization when burial took place. On the other hand, the marks on the teeth are somewhat problematic; some are located on the roots, implying that the teeth had fallen out of the skull when the marks were produced. The teeth were recovered close to the vault fragments and, according to the 3D reconstruction of the burial position, close to the rest of the skeleton. This suggests that the teeth are more likely to have detached from the skull while in the

secondary deposit, after burial occurred, due to post-depositional process(es). If they had detached before, the chances that they would have been deposited by the debris flow close to the skull are extremely low. One hypothesis is that MH1 remained long enough in the primary deposit for the teeth to fall out. Only then did the insects leave traces on the teeth, which were separated from the skull. Alternatively, the damage was caused much more recently, but before the deposition of manganese, in the decalcified sediment, from where the teeth come from. In the last case, the insect damage does not provide information about the timing of exposure in the primary deposit. In both cases, the location of the damage on the roots of the teeth, combined with the total absence of insect modification on the rest of the skull, raises the question of what motivated the insects to modify the fossils. If the marks are associated with feeding, then the makers were not after organic nutrients, but rather minerals. In this regard, the hypothesis of hide beetles feeding on remnant dry matter does not hold up. It follows then that either another species of insect interested in the mineral content of the fossilized teeth modified them, or tunnelling insects, which considered them an obstacle, displaced the teeth.

Finally, on the left ilium, the insect modifications are on top of the manganese, which implies that they were produced after fossilisation. These traces indicate recent insect activity at the site, which is significant in terms of understanding the fossil deposit in the context of a modern environment, but does not provide any information regarding the timing of decomposition and burial of MH1.

### *3.2.4. Summary*

The slight to moderate cracks of weathering, the level of disarticulation, as well as the possible occurrence of ancient insect damage, indicate that MH1 was in an advanced stage of decay when he was buried. The same external conditions as for MH2 must have prevailed and contributed to slow down the decomposition process (body placed in the shade, no disruption by scavengers, no significant temperature fluctuations, and probably

limited access to the carcass for insects). Therefore, the decomposition must have taken roughly the same time for MH1 and for MH2 to be completed.

### *3.2.5. Did MH1 and MH2 enter the cave at the same time?*

The question of whether MH1 and MH2 entered the cave system at the same time is difficult to answer in a definitive manner. However, several aspects of the taphonomy of both individuals provide some elements of response. Noticeable variations are observed between the juvenile male and the adult female in terms of weathering stage and degree of articulation of their bones, which can either indicate a different time of entry (MH1 entering first and spending more time inside the primary deposit than MH2) or microvariations inside the primary deposit, and internal differences, such as the age difference, having an impact on the rate of decomposition and disarticulation (MH1 and MH2 entering the site together). There is, however, as far as we know, no published study having demonstrated a fastest rate of disarticulation for juvenile hominin individuals compared to that of adult ones.

Weathering stage

A comparison between MH1 and MH2 fossils shows differences in the general weathering patterns of the two individuals, with MH1 being slightly more weathered than MH2 (see Chapter 6). This could imply a longer time of exposure in the primary deposit for MH1 than for MH2, and consequently an earlier entry into the cave system. It could also be caused by local variations inside the cave chamber affecting the conditions of decay and preservation, leading to differences in the weathering between MH1 and MH2 – without necessarily indicating a different time of exposure. Furthermore, both individuals show internal variations in terms of weathering of their bones, which are as significant as the variations observed between the two. For each individual, elements recovered from the same block, in close proximity, show different stages of weathering (e.g. ribs with weathering stage 2 and long bones of the right arm with weathering stage 1, from the

“arm block” for MH2; cervical vertebrae, right ulna, mandible and fragment of ilium with weathering 1 and right clavicle, fragment of right ilium and fragment of left ischium with weathering 2, from the “clavicle block” for MH2). Some bones might have been exposed more than others given their position (toward the ground or facing the surface), or the quantity of soft tissue remaining on them (bones with no skin protecting them versus elements covered by dry skin). Consequently, the differences in weathering between MH1 and MH2 cannot be used as an argument in favour of a different time of entry into the cave system for the two individuals.

Degree of articulation

There is a clear difference between MH1 and MH2 in terms of degree of articulation; while MH2 preserves numerous elements articulated or in anatomical proximity, MH1 does not preserve any. However, if MH1 was completely disarticulated before the debris flow occurred, his bones would have been scattered inside the secondary deposit. On the contrary, very little movement is observed for MH1 remains in Facies D. His bones are all found in close proximity, with the exception of the two metatarsals, the attribution of which is discussed in Chapter 9. The general anatomical position is maintained. This suggests that his bones were still at least loosely held together possibly by dry skin (natural mummification) when the debris flow that buried the skeleton occurred. Complete disarticulation and slight displacement took place post-burial, in the secondary coarse sand deposit. Therefore, the differences in the degree of articulation between MH1 and MH2 do not seem to reflect a difference in the timing of entry inside the cave system. Age could be an important factor influencing the degree of disarticulation, with the adult female having stronger articulations that take longer to dislocate than the younger male.

### 3.3. Final burial position

MH1 is buried in a different pose and orientation to MH2 (perpendicular to it), head first towards the south-west, and rest of the skeleton lying with the lower limbs extended along the body, and the right arm flexed. Based on the hypothetical 3D reconstruction of the position of MH1 inside Facies D, it is proposed that the skeleton came to rest with the head lying on its left side and facing north (Figure 8.5). The general location of the right elements compared to the left elements suggests that the body was lying on its belly. The right elements (right humerus, right clavicle, right hemi-mandible and fragments of right pelvis) are all positioned to the south of their corresponding left elements (left mandible, left clavicle, left humeral head and left ilium) (Figure 8.5). The femurs are the only exception to that rule, but considering that the right femur was recovered isolated in an *ex situ* block of sediment, with no direct link to another element of the MH1 skeleton, its position in the deposit is purely hypothetical.

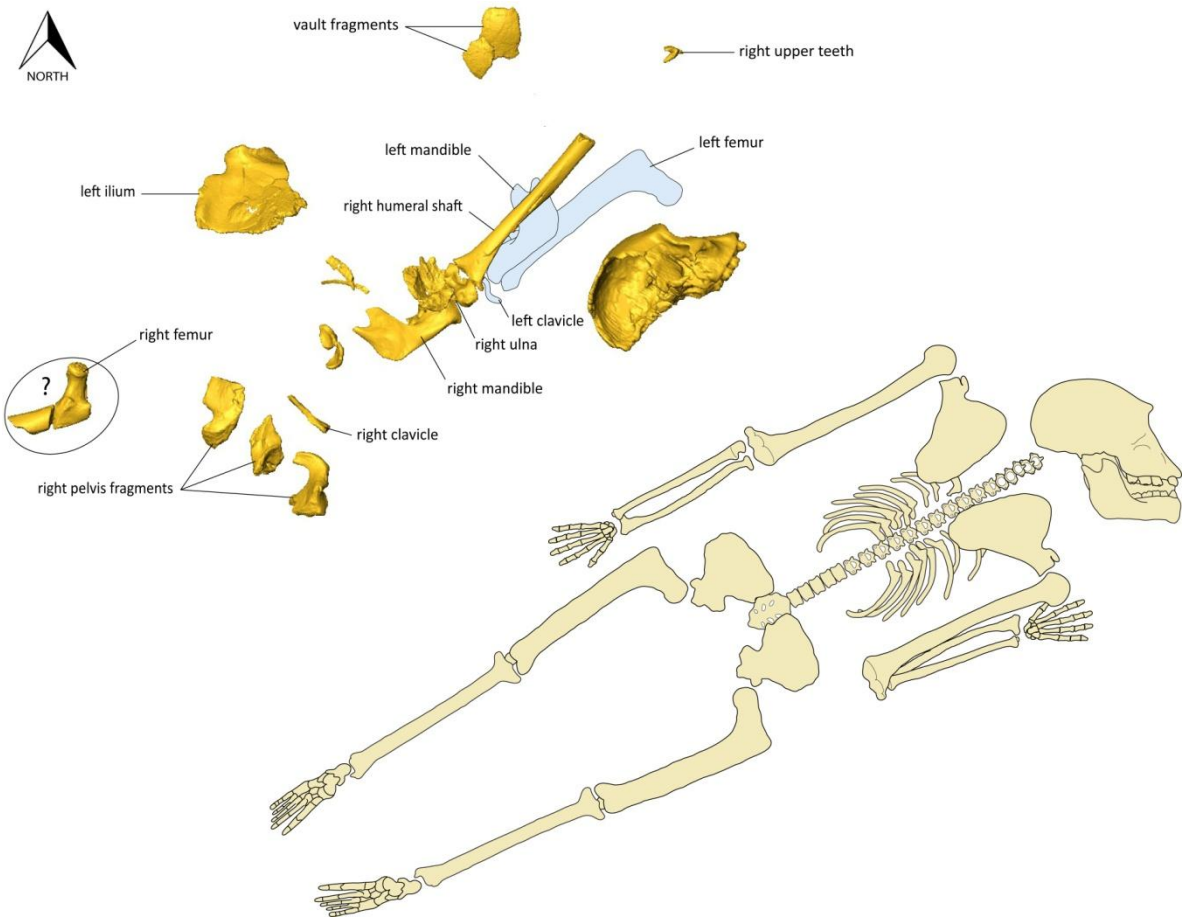



**Figure 8.5.** Burial position of MH1 in the deposit, viewed from the top (upper left corner: burial position as recovered from the deposit, including only the bones that were found; bottom: hypothetical burial position, before displacement and including the missing bones). The bones in blue are the ones identified inside the unprepared block UW88-B051.

The absence of green stick impact fractures, or at least locally depressed bone with evidence of trauma, suggests that the breakage of the skull did not happen because of the death trap fall. However, the cracks on top of the skull are consistent with breakage that happened when the skull bones were still fresh, pre-fossilisation (L. Berger, pers. comm.). This suggest compression and distorsion of the buried skull by the weight of sediments in the secondary deposit, saturated and drying, and collapse of blocks from the roof, post-burial, but before an advanced and set stage of diagenetic alteration had taken place. The carcass came to rest at the position where the cranial vault fragments were discovered. It is likely that at that place, the skull hit a rock during transportation, breaking the right

vault. While there is little other evidence of transportation, movement with force seems a reasonable explanation in the sequence of events. If one accepts that the skull is in its original burial place, then the pelvis, humeri, and right ulna do not seem to have moved from their original position. Some slight movement, from southwest to northeast and from northeast to southwest, occurred after deposition and can explain the dispersal of the bones (e.g. displacement between skull, vault fragments and upper front teeth, dislocation of the mandible, movement of the clavicles and displacement of the left femur).

The same argument can be applied to the front teeth (right incisor and canine). They are complete and there is no indication of fracture or breakage on the front of the maxilla. The teeth probably did not detach due to the fall, but later, after decomposition of the periodontal tissue, during the movement caused by the debris flow in the secondary deposit, just before burial (this is confirmed by the occurrence of insect modifications on the roots of the teeth; see above). This would explain the short distance observed between the vault fragments and the teeth, recovered only 29 cm away from each other in the deposit. It implies that the insects were active in the burial deposit before fossilisation, which also means, for hide beetles anyway, that the deposits were not immersed in a pool of water.

As for MH2, the hypothetical burial position of MH1, shown in Figure 8.5, seems to be consistent with a natural death posture, also most likely close to the position in which the individual died. There is no indication of hyper flexion, *rigor mortis* or trace of agony. The fact that the right arm of MH1 was flexed suggests that the body was lying on the ground and did not decompose in water, in which case, all limbs would have extended, in a floating position. The same conclusions as the ones proposed for MH2 can be drawn. In other words, if there was a debris flow, it must have occurred after MH1 was skeletonised and mummified, and the position in which he died was maintained by dry skin and tendons. Alternatively, there was no debris flow and MH1 would have decomposed on the

ground in his death posture, mummified and been progressively covered and buried by infilling sediments.

## 4. TAPHONOMY OF THE FRAGMENTARY HOMININS MH3, MH4, MH5 AND MH6

### 4.1. Introduction

The state of preservation of MH3, MH4, MH5 and MH6, referred to as "fragmentary hominins" (to differentiate them from the near complete MH1 and MH2 individuals), is very different from that of MH1 and MH2, and implies a different combination of taphonomic processes for their accumulation mode and fossilisation. None of them preserves complete bones or elements in articulation. They are only represented by a few elements each, and the bone surface is not well preserved. Here, different hypotheses are proposed to explain the taphonomy of MH3, MH4, MH5 and MH6. I argue that it is currently not possible to favour any of the following hypotheses over another one, given that some *in situ* deposits as well as *ex situ* calcified breccias remain to be excavated and/or prepared.

### 4.2. Excavation bias

The first hypothesis concerns the limitations of a small sample size and the fact that extensive excavations of *in situ* sediments have not yet been undertaken. Thus, MH3-MH6 may only be represented by a few elements because their missing bones have not yet been recovered, and are still embedded either in *ex situ* blocks of sediments not yet prepared, or *in situ*. According to this hypothesis, no definite taphonomic hypothesis can be proposed for MH3, MH4, MH5 and MH6, until the deposit is fully excavated.

### 4.3. Different accumulation processes

Another hypothesis concerns how the fragmentary bones of the hominins entered the cave. Instead of individuals falling inside the cave, through a vertical shaft, as is the case for MH1 and MH2, some hominin specimens could have come from the surface, in

the forms of fragmentary and weathered bones, collected by rain and gravity, from individuals who died and decomposed outside the cave. Alternatively, the poorly preserved hominins (MH3-MH6) could have been accumulated by a more damaging agent, such as a carnivore, leading to significant destruction of the bones and the recovery of fragmentary elements only. There is, however, little evidence supporting this hypothesis so far: no definitive carnivore tooth mark has been observed on the hominin bones and the sample is too small to discern any general pattern in terms of mortality profile or skeletal element survival.

### 4.4. Different timing of burial

The third hypothesis proposes that the hominins MH3-MH6 entered the cave through a natural death trap, as MH1 and MH2, but earlier. They would have therefore been in a more advanced state of decomposition and disarticulation. Furthermore, as explained previously, the desiccation process is extremely dependant on several variables that were not necessarily present in all areas of the cave. Therefore, MH3-MH6 might not have mummified in the same way as MH1 and MH2. When the debris flow carried them, it could have had a more important impact in terms of dispersal of the bones, explaining the small number of elements recovered for each of the fragmentary hominins. This, combined with the lack of extensive excavation of the *in situ* deposits, might explain the absence of the missing elements for these individuals.

# Chapter 9. Implications for the past and for the future: discussion of the results.

Some of the implications of the results described previously are presented in this final chapter. The understanding of the taphonomy of the hominins, especially the spatial analysis and reconstruction of their burial position inside the deposit, permits a discussion of the re-assignment of some of the disarticulated and *ex situ* hominin remains, as well as predictions of the location of missing skeletal elements. A strategy for future excavations is offered, including a detailed technical guideline based on the knowledge acquired during the course of this research. Finally, consideration is made of some of the research questions that remain to be explored.

## 1. WHERE ARE THE MISSING REMAINS?

The taphonomic scenario proposed for MH1 and MH2 (fall inside a vertical shaft, decomposition without major disruption by taphonomic agents, and probable natural mummification before burial), implies that both skeletons were complete or near complete when they were buried. Consequently, all their remains should eventually be recovered. This observation, combined with the hypothetical position of the bodies at the time of burial, allows for the making of predictions and suggestions regarding the location of the missing remains, whether *in situ* or in blocks of calcified sediment (see below Table 9.1 for a summary)

### 1.1. MH1 missing remains

The hypothetical position of the missing remains is based on the assumption that the MH1 body was lying on its belly, head towards the south at the top of Facies D, with the right elements on the northern/north-western side and the left elements on the southern/south-eastern side (see Chapter 8, Figure 8.5).

### *1.1.1. Right hand*

All elements of the right hand are missing, except one near-complete metacarpal (UW88-112). In the hypothetical 3D reconstruction, the right arm (humerus and ulna) is facing towards the north, in other words towards the *in situ* deposits, on the eastern side of Facies D. Therefore, it seems reasonable to propose that the missing right hand is still embedded in the deposit, close to where the right ulna comes from. However, the joints that hold the hand bones together are amongst the first ones to disarticulate (Duday, 1990, 2009; Maureille and Sellier, 1996), and MH1 does not preserve any articulated elements, so it seems unlikely that the right hand will be recovered as an articulated unit, such as the right hand of MH2, but rather more dispersed.

### *1.1.2. Left arm*

Only the left humeral head was recovered, inside the skull block. Given the general position of left elements towards the south of the deposit (i.e. area that has undergone some mining; see Figure 8.5), it is likely that the missing left humeral shaft, radius, ulna and hand, are inside one or several blocks of calcified sediment already removed by the miners, but not yet prepared. A possible humeral shaft and a possible distal humerus identified inside the block UW88-B051 could represent the missing left humerus of MH1. Their position, just south of the right humerus, is consistent with where the left arm is expected to be found. The preparation of the block will provide a more definitive answer.

### *1.1.3. Lower limbs*

<u>Feet</u>

Elements of the right foot of a hominin have been identified in the *in situ* sediments in the area where the MH1 *in situ* remains were recovered. Five possible foot or hand bones have been identified inside the unprepared block (UW88-B051). Most bones from this block belong to the left side (femur, mandible, possibly clavicle and

humerus), while most right elements of the skeleton were found towards the north of the deposit (see Chapter 8, Figure 8.5). Block B051 refits in the southern part of the volume of sediment where MH1 comes from. The left foot is likely to be more south of the right one. Therefore, the foot or hand bones from block UW88-B051 could belong to the missing left foot of MH1. This remains to be confirmed with further preparation of the block.

Tibiae

A possible tibia was identified inside the unprepared block UW88-B051, which contains mostly elements for the left side; the possible tibia could be the missing left tibia of MH1. If not, and if the legs of MH1 were fully extended, both tibiae should be located towards the north-east relative to where the vault fragments were recovered. They might still be embedded inside the deposit. If the legs were flexed, then the tibiae should be just close to the area where the skull comes from, which corresponds to sediment that was removed by the miners. In this case, the tibiae should be looked for inside *ex situ* blocks.

#### *1.1.4. Sacrum*

All vertebrae attributed to MH1 were recovered from *ex situ* blocks, as were fragments from the right and left pelvises. It seems likely that the sacrum will therefore also be found in a block already removed by mining, but not prepared yet.

### 1.2. MH2 missing remains

The following hypotheses for the location of MH2 missing remains are based on the reconstruction of the body position inside the deposit, lying on its back, with the head towards the south and the bottom of Facies D, the arms along the body, and the legs flexed with the knees pointing east (see Chapter 7, Figures 7.29-35 and Chapter 8, Figure 8.4).

### *1.2.1. Left leg and pelvis*

The position of the right femur in the arm block and the proposed position of the right ankle are consistent with the legs flexed with the knees pointing east and the feet towards the west. The right leg is below the left leg. This is consistent with a logical anatomical position, and is confirmed by the absence of elements from the left leg in the arm block, even after preparation. The missing elements of the left leg (femur, patella and foot bones), on the top of the "arm block", are therefore very likely to have been blown away during the mining of the site. These elements should be found in one or several blocks of calcified sediment removed by the miners and not yet prepared. Some elements from the left side have already been recovered in some of the *ex situ* blocks, such as the left fibula (specimens UW88-23 and 84), tibia (specimen UW88-24), pelvis (specimens UW88-10, 135 and 134), and pedal proximal phalanx (specimen UW88-91).

### *1.2.2. Skull and first cervical vertebrae (atlas and axis)*

The mandible and three cervical vertebrae were recovered associated with the arm block, whereas the skull, the atlas and axis are missing. The mandible/temporal joint in human skeletons is unstable and disarticulates early in the decomposition process; the articulation between the skull and the atlas on the other hand is a persistent articulation (Duday, 1990, 2009; Maureille and Sellier, 1996). The MH2 skeleton in Facies D shows very low bone dispersal and movement, the majority of the bones being in association inside the arm block. Two hypotheses are proposed regarding the possible location of the missing skull and first cervical vertebrae. These hypotheses are related to the moment when the skull detached from the rest of the body, whether before transport by the debris flow from the upper chamber to the lower one, or during transport.

Hypothesis 1: disarticulation of the skull before disturbance by debris flow

The first hypothesis proposes that the skull and associated atlas and axis disarticulated from the rest of the body in an early stage, while the skeleton was still decomposing in the primary deposit, before the debris flow. Therefore, when the flow occurred, the body was transported separately from the skull. In this case, it is difficult to predict the position of the skull inside the deposit. With the exception of Voorhies's experience (1966), human skulls belong to the transportable group and are, within this group, the fastest moving elements (Boaz and Behrensmeyer, 1976). Experiments with sheep and macaques indicate the same (Coard and Dennell, 1995; Coard, 1999). The skull of MH2 could therefore have been transported to the extreme bottom part of the chamber, which is the southern part of the actual cave, and also the mined area. Depending upon its condition, and the nature of the flow, it could also have sunk to the bottom of a low-density waterlogged sandy secondary deposit. In other words, the skull could either still be still inside the deposit, anywhere in Facies D, or in one of the blocks removed by the miners.

Hypothesis 2: disarticulation of the skull due to debris flow

The second hypothesis suggests that the skull was still partially articulated with the rest of the body and moved together with it in the debris flow. It would only have detached when the body reached the bottom of the lower chamber and collided with the flowstone. The impact would have detached the skull, together with the atlas and axis, from the rest of the body. The skull could then have remained in close proximity to the body.

Discussion

The articulations between the skull and the mandible and between the skull and the cervical column are classified as unstable and are amongst the first ones to disarticulate in an undisturbed decay process (Duday *et al*., 1990, 2009; Maureille and Sellier, 1996). The

skull could have detached at an early stage, before the body was moved to the bottom of the deposit. However, other unstable articulations, such as the right femoral head and the acetabulum, the right patella and tibia, the right humerus and scapula, and the manubrium close to the clavicle, have been preserved during transport, burial and fossilisation. Furthermore, the articulation between the mandible and the temporal is an unstable articulation and tends to disarticulate *before* the skull detaches from the vertebral column (Duday, 2009). In other words, if the skull had disarticulated from the cervical column in the upper chamber, then the mandible would also have disarticulated. Consequently, the transport would have dispersed both the skull and the mandible, but the fossil evidence shows the contrary, namely that the right mandible is still very close to its anatomical position, since it was recovered associated with the upper body (i.e. it was found in the "scapula fragment block", which refits directly with the scapula and associated bones from the "arm block"). This suggests that the skull was still articulated with the rest of the body when the debris flow carried it. I propose that the skull was still attached to the cervical column when transported and that the mandible was still attached to the skull. The skull would only have detached from the mandible when the skeleton impacted the flowstone. This implies that the skull should be very close to where the mandible was recovered, either inside the "arm block", in a part that has not been prepared yet, or in a block of breccia coming from the same area as the "arm block".

### *1.2.3. Left upper limb*

Some elements from the proximal and distal parts of the left upper limb were recovered, namely two fragments of the left scapula (UW88-103 and UW88-104), the distal part of the left clavicle (UW88-94), the proximal left humerus (UW88-101), some left carpals (UW8-105, 106, 107), and a left metacarpal (UW88-182). Only the left humeral shaft, radius and ulna are missing. The missing left carpals are present *in situ* in the west-northern part of where the "arm block" was recovered. The right arm was preserved in an extended position. Consequently, it seems very likely that the missing left elements (i.e.

humeral shaft, radius and ulna) were located to the left of the "arm block". They should be preserved in blocks already removed by mining and still awaiting preparation.

**Table 9.1.** Hypothetical location of the missing hominin remains.

| Individual | Elements | *Ex situ* block(s) | *In situ* deposits |
|---|---|---|---|
| **MH1** | right hand | | close to where the vault fragments were recovered eastern side of the deposit? |
| | right foot | | |
| | tibiae | block B051 and/or other block? | |
| | left arm | block B051 or other block | |
| | left foot | possibly block B051 | |
| | sacrum | isolated block | |
| **MH2** | left pelvis, leg and foot | one or several block(s) | |
| | skull, atlas and axis | "arm block" or separate block | |
| | left arm | isolated block | |

## 2. REATTRIBUTION OF SOME REMAINS

Three hominin remains attributed to MH1 and MH2 were recovered *in situ* in Facies D, but very far from the others: a fibula shaft fragment (specimen UW88-202) attributed to MH2, and two right metatarsals (UW88-16 and UW88-22) attributed to MH1. Their preliminary association with MH2 and MH1 is discussed here.

### 2.1. MH1 metatarsals

Two right metatarsals, recovered together *in situ*, were preliminary attributed to MH1, based on their size. UW88-22 is a definite right fourth metatarsal of a hominin (Zipfel *et al*., 2011), with the distal head missing, either because it was unfused, consequently belonging to a juvenile individual, or because it is damaged, in which case age estimation is not possible (J. DeSilva, pers. comm.). UW88-16 is most likely hominin, and most likely a right fifth metatarsal (J. DeSilva, pers. comm.). This specimen is fragmentary and misses both distal and proximal epiphyses; it is therefore impossible to establish whether or not they were fused. The hypothetical reconstruction for the position of MH1 position in the deposit indicates that it was lying horizontally, with the head facing south and the rest of the body, including the legs facing east. Both metatarsals were found

on the extreme *west* side of Facies D, 142 cm away from the other MH1 *in situ* remains, and higher up in the deposit (Figure 9.1), which is in contradiction with the general low level of dispersal observed amongst all *in* and *ex situ* MH1 remains (see Chapter 7), and with the position of the body inside the deposit. Based on these elements, I suggest that UW88-16 and UW88-22 might belong to another, as yet unidentified, individual.

### 2.2. MH2 fibula shaft fragment

A fibula shaft fragment, side indeterminate, also recovered from Facies D, was preliminarily attributed to MH2. It does not refit directly with any other fibula fragment attributed to MH2, nor does it overlap with any of them. Since it is a shaft fragment, it is not possible to comment on the degree of fusion of the epiphyses and therefore to propose an age estimate. The location inside the deposit (380 cm away from the centre of the arm block: see Chapter 7 and Figure 9.1) is not consistent with the very low dispersal rate observed for all *in situ* and *ex situ* MH2 bones (Figure 9.1). Several other incomplete and as yet undescribed adult hominins (MH4 and MH6) have been identified at the site. I therefore propose that the fibula fragment UW88-202 does not belong to MH2, but to another hominin.

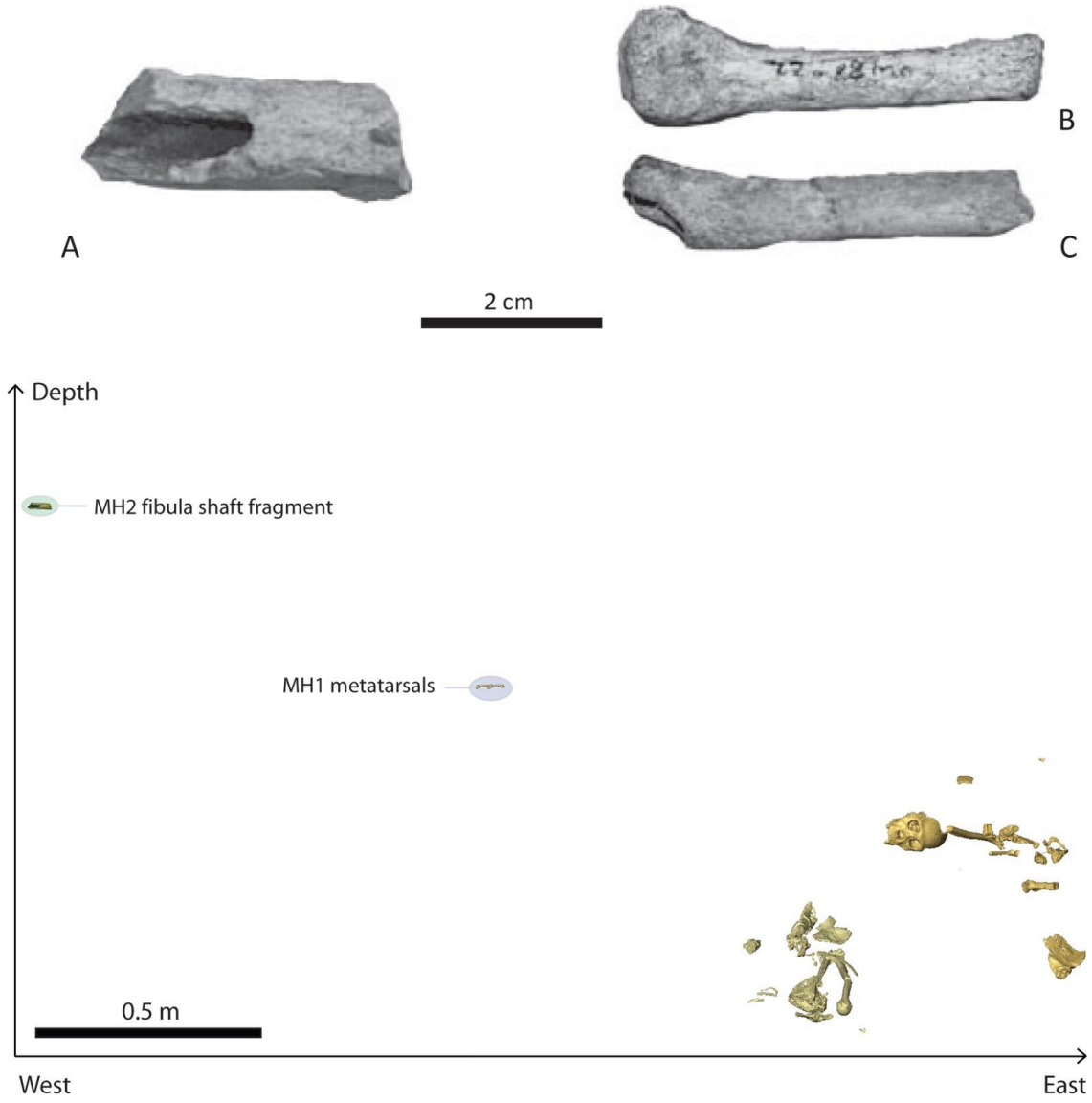



**Figure 9.1**. Position in the deposit of the *in situ* fibula shaft fragment (A: specimen UW88-202, attributed to MH2) and metatarsals (B: specimen UW88-22; C: specimen UW88-16; attributed to MH1), in relation to MH1 and MH2 remains (viewed from the south). UPDATE

## 3. TECHNICAL GUIDELINE FOR FUTURE EXCAVATIONS OF *IN SITU* DEPOSITS

Excavations of *in situ* deposits in Pit 1 and Pit 2 will start in the near future. They will help in answering many questions regarding the general taphonomy of the faunal assemblage, and provide more information concerning the taphonomy of the hominins. Various points of interest, such as similarities and differences between the fossil-bearing

facies in terms of preservation and taphonomy, timing and exact mode of deposition of these units, and extent of the deposits, will be explored.

One of the outcomes of this research project is to highlight the importance of recording exhaustively and precisely spatial data, for the reconstruction of the burial position specifically, and for the understanding of the taphonomy of the fossil assemblage more generally. Therefore, all information regarding the exact provenance, position, orientation and direction in the deposits of the bones is crucial and must be recorded, especially since excavations are a destructive process. If not saved, once the bones are removed from the deposit, this information is lost. Some remains belonging to MH1, MH2 and possibly the fragmentary hominins MH3-MH6 are still embedded inside *in situ* deposits. Their orientation and exact position in the sediments will help complete the virtual 3D model, and confirm or refute some of the assumptions made regarding the exact burial positions, at least for MH1 and MH2, and the taphonomic history for the other hominins.

The nature of the sediment at the site makes excavation procedures more complex than in sites where the units are composed of decalcified material, easy to remove and offering a better control of the advance of the dig. This constitutes a supplementary reason to ensure that, at Malapa, all field and spatial data are recorded *during* the excavations, for instance by multiplying the methods of recording (coordinates, pictures, notes, drawings), even if, and in order that, they overlap.

The following points would be useful to consider for future excavations:

First, for every single fossil, all information regarding the provenance and position must be recorded, namely whether the specimen comes from *in situ* or *ex situ* sediment, its facies of origin and coordinates (when found *in situ*); and for the elongated specimens, including elongated stones, its orientation, direction and angle, and the part on which it is lying (e.g. medular cavity versus cortical bone, dorsal versus ventral side). The nature of

the sediment implies that most specimens will be removed in the laboratory and that only blocks will be removed from the *in situ* deposits. It is therefore even more important to make sure that all information allowing the refitting of the blocks back to the deposit is preserved. Pictures can be useful, but they need to be standardized and informative, for instance they must have a scale, a compass and a legend (with the date, the number of the specimen/block, the facies) on the picture. It might sound tedious to have every block that is removed sketched, but drawings are extremely useful because all kinds of information can be annotated. They can also be easily manipulated, referenced, and revised as the excavations proceed. A manual and daily note book recording every event of the excavations is also very useful. A record of the progress of the excavations should be conducted daily, in order to prevent any mistakes in the coordinates, any omission in the data recorded, and any problem.

One of the difficulties that was encountered during the analysis of the material in this study was the impossibility of tracing some specimens back to their exact location. It is recommended that the most straightforward possible numbering system be used to avoid confusion. Ideally a fossil identified at the site receives a number *at the site*, together with a tag containing the information previously mentioned. The specimens should keep the same number from their recovery at the site, all the way to the final database. The same goes for the blocks, which will more likely represent the majority of the elements removed from the site.

## 4. RESEARCH PERSPECTIVES

### 4.1. Future applications of the palaeoforensic approach

The palaeoforensic approach, combining analysis of bone surface modifications, general preservation pattern and spatial data, with the aim of reconstructing the burial position of a skeleton, was developed in this research project to study the case of the two well-preserved hominins (MH1 and MH2). In future, the same approach could be applied to other well-preserved and complete skeletons from the Malapa site, either skeletons

found *ex situ* (bovid skeletons for instance) and for which refitting into the deposit is possible, or skeletons that will no doubt be recovered from the *in situ* deposits during upcoming excavations (hominins and non-hominins).

This innovative approach could also be applied to other well-preserved and near complete skeletons of early hominins, for which spatial data are available and that have not been subjected to destructive post-depositional processes, such as StW 573 "Little Foot" from Sterkfontein Member 2. I also suggest that a palaeoforensic approach should from now on be systematically followed for any well-preserved skeleton of an early hominin discovered, given the amount of information that can be provided.

## 4.2. Unsolved research questions about the taphonomy at Malapa

Several points of interest could only be touched upon during the course of this research project, since an *in situ* and more complete faunal assemblage is required in order to address them properly. Four questions of interest for the general understanding of the taphonomy of the site and faunal assemblage have been selected. These questions have not yet been resolved, and will hopefully find answers as excavations proceed and *in situ* faunal material is recovered. The first three points have already been mentioned in Chapter 8. The last point offers a reflection about one aspect that has not been considered previously in this thesis.

### *4.2.1. What happened to the fragmentary hominins?*

Because some bones belonging to MH3, MH4, MH5 and MH6 might still be embedded inside the deposits, it is difficult to compare their taphonomic characteristics with that of MH1 and MH2. They could share a common mode of accumulation, burial and fossilisation, if it becomes evident that they are also represented by complete bones, articulated elements and well-preserved bone surfaces. On the other hand, if no other elements belonging to these individuals are revealed through excavations, another

sequence of events will have to be considered to explain their different state of preservation.

### *4.2.2. Was there really a debris flow?*

The preliminary hypothesis of a single debris flow event transporting both the hominins and associated material to the bottom of the cave system (Dirks *et al*., 2010) is being challenged by the results of this taphonomic analysis of MH1 and MH2. Several elements are not in keeping with the action of a single significant and sudden influx of water into the cave. The analysis of the taphonomy of new *in situ* faunal material, especially a spatial study of bone distribution and orientation inside the deposit, microscopic observations of the bones to identify evidence for water abrasion, and quantitative estimates of skeletal parts preserved to determine whether or not there is fluvial sorting, will provide information to determine if water flow played a major role in the accumulation process and burial of the faunal assemblage at Malapa. A detailed comparison of the taphonomy of the fauna between the different facies, combined with a sedimentological fabric analysis of the sediments from these facies, should prove decisive in the question of the action of the debris flow.

### *4.2.3. What is the exact nature of the role played by insects and who are they?*

Insect damage was identified on numerous bone fragments, including some hominin remains. The identity of the species that produced the modifications is not clear at the time of writing. There seem to be two distinct categories of insect damage, on fresh bones (or at least before the deposition of manganese on the bones) and on fossils (on top of the manganese). Interestingly, both categories present the same features (intersecting striation marks, pits, star-shape pits, small borings and surface gnawing), which seem to indicate that they were produced by the same type of insect, but at two distinct moments in time. The very significant difference in the proportions of insect damage between bones recovered from calcified sediment and those recovered from

decalcified sediment seems to be informative of a biotic process at work. More investigations are required to determine why the insects modified the remains in fresh and fossilized states of preservation. Understanding the role played by insects, and the timing of their involvement will help the identification of their impact on the taphonomy of the fossil assemblage and site (e.g. displacement of fossils inside the deposits, reworking of sediments, and possible destruction of the original stratigraphy).

### *4.2.4. Where are the other primates?*

Comparison with other Plio-Pleistocene cave deposits

Around two million years ago, five known species of early hominin, namely *Australopithecus africanu*s, *Australopithecus* "second species", *Paranthropus robustus*, early *Homo,* and *Australopithecus sediba* inhabited the Cradle of Humankind. Their remains have been recovered from several cave deposits in the region: Sterkfontein, Swartkrans, Kromdraai B, Cooper's D, Gladysvale, Drimolen and Gondolin A (for more details and complete references, see Chapter 2, Table 2.1). Most fossil-bearing sites have yielded specimens attributed to a single species, but in some cases, the remains of two species have been found inside the same deposit. Hence, Swartkrans Member 1 (Lower Bank and Hanging Remnant) and Member 2 contain specimens attributed to *P. robustus* and to *Homo* sp. (Brain, 1981; Grine, 1989, 1993, 2005; de Ruiter, 2003), while at Sterkfontein Member 4, the early hominin fossils have been attributed to both *Au. africanus* and *Au.* "second species" (Dart, 1925; Broom, 1936; Brain, 1981; Pickering, 1999; Clarke, 1988, 1998, 1999, 2008).

Large-bodied non-hominin primates are also present in the Sterkfontein Valley around 2 Ma. In the cave deposits of that region, the remains of various papionins (Family Cercopithecidae, Sub-Family Cercopithecinae) have been recovered (Broom and Robinson, 1949; Freedman, 1957, 1976; Brain, 1981; Watson, 1993; McKee and Keyser, 1994; Pickering, 1999; Keyser *et al*., 2000; de Ruiter, 2001, 2003; Lacruz *et al*., 2002; Kibii, 2004,

2007; Pickering *et al*., 2004a, 2004b; Adams, 2006; Gilbert, 2008; Gommery *et al*., 2008; de Ruiter *et al*., 2009) (Table 9.2). These include the extinct giant gelada, *Theropithecus oswaldi*, extinct large baboons *Papio (Dinopithecus) ingens*, *Papio izodi, Papio angusticeps*, and *Gorgopithecus major*, the extinct baboon *Papio (hamadryas) robinsoni*, and the extinct *Parapapio (i.e. Parapapio jonesi, Parapapio broomi, and Parapapio whitei)*, related to modern mangabeys (Gilbert, 2008) (Table 9.2).

**Table 9.2.** Extinct and extant papionins found in deposits from the Cradle of Humankind.

| Species | Deposit | Reference |
|---|---|---|
| *Papio (hamadryas) robinsoni* | Swartkrans M1 LB, HR, M2, M3; Cooper's D; Drimolen; Bolt's Farm (Femur Dump); Kromdraai A | Freedman, 1976 ; Brain, 1981 ; Keyser *et al*., 2000 ; de Ruiter, 2003 ; Gommery *et al*., 2008 ; de Ruiter *et al*., 2009 |
| *Papio (Dinopithecus) ingens* | Swartkrans M1 LB, HR, M2 | de Ruiter, 2003 |
| *Papio izodi* | Sterkfontein Member 2; Jacovec Cavern | Pickering *et al*., 2004a; Kibii, 2007 |
| *Papio angusticeps* | Minnar's; Kromdraai A and B; Haasgat | Freedman, 1957, 1976; Brain, 1981; McKee and Keyser, 1994 |
| ***Papio* sp.** | **Malapa** | **unpublished** |
| *Parapapio jonesi* | Swartkrans M1 HR; Sterkfontein M2, M4; Jacovec Cavern | de Ruiter, 2003; Pickering *et al*., 2004a ; Kibii, 2007 |
| *Parapapio broomi* | Sterkfontein M2, M4, Jacovec Cavern; Bolt's Farm | Brain, 1981; Freedman, 1976; Pickering *et al*., 2004a; Kibii, 2007 |
| *Parapapio whitei* | Sterkfontein M4 | Brain, 1981 |
| *Theropithecus oswaldi* | Swartkrans M1 LB, HR, M2, M3; Cooper's D; Sterkfontein M5 (StW 53 Breccia and Oldowan Infill) | de Ruiter, 2003 ; Pickering, 1999 ; Ruiter *et al*., 2009 |
| *Gorgopithecus major* | Kromdraai A; Cooper's D | Broom and Robinson, 1949; Freedman, 1976 ; Brain, 1981 |

*HG: Hanging Remnant; LB: Lower Bank, M: Member, StW: Sterkfontein.*

Hominin and non-hominin primates are usually found associated in the deposits, with a variable percentage for each group (Table 9.3). In the faunal assemblages recovered in deposits from the Cradle of Humankind, non-hominin primates are *always* more abundant than hominins, in terms of NISP. Swartkrans Members 1 (Lower Bank) and

2 are the only exceptions, where hominins are more abundant than the papionins in terms of MNI (Brain, 1981; Watson, 1993; de Ruiter, 2001) (Table 9.3 and Figure 9.2). The abundance of primates (hominins and non-hominins) in the fossil cave deposits is usually interpreted as evidence for the "carnivore-collecting hypothesis" (Brain, 1981), and more specifically specialized predation upon primates by leopards and hyaenas (de Ruiter, 2001; Carlson and Pickering, 2003; Pickering *et al*., 2004b, 2004c; Clarke, 2007; Kibii, 2007).

At Malapa, the ratio of hominin to non-hominin primates is extremely high, constituting a notable exception within the context of Plio-Pleistocene South African cave deposits (Table 9.3 and Figure 9.2).

**Table 9.3.** Abundance of hominin and non-hominin primates (NISP/MNI) in Plio-Pleistocene faunal assemblages from the Cradle of Humankind.

| Site | Deposit | Hominins | Cercopiths | Reference |
|---|---|---|---|---|
| SWARTKRANS | M1 HR | 279/90 | 423/117 | Brain, 1981; Watson, 1993; de Ruiter, |
| | M1 LB | 46/16 | 240/9 | 2001 |
| | M2 | 52/24 | 217/12 | |
| | M3 | 27/11 | 384/15 | |
| STERKFONTEIN | Jacovec Cavern | 12/6 | 314/13 | Kibii, 2007 |
| | M4 | -/87 | -/298 | Brain, 1981; Pickering *et al*., 2004b |
| | M5 StW 53 Breccia | 14/2 | 50/7 | Pickering, 1999 |
| | M5 Oldowan Infill | 5/2 | 187/8 | |
| | M5 West Infill | 7/4 | 10/4 | |
| KROMDRAAI | A | -/- | 95/14 | Brain, 1981 |
| | B | 8/6 | 495/37 | |
| COOPERS | D | 7/2 | 431/15 | Val *et al*., submitted |
| GONDOLIN | GDA | 2/2 | 3/1 | Adams, 2006 |
| GLADYSVALE | GVED | 1/1 | 12/2 | Lacruz *et al*., 2002 |
| **MALAPA** | **-** | **256/6** | **1/1** | **Dirks *et al*., 2010 ; Kuhn *et al*., 2011 ; currently under study** |

*GVED: External Deposits, HG: Hanging Remnant, LB: Lower Bank, M: Member, StW: Sterkfontein.*

While 256 hominin remains, representing a minimum number of 6 individuals, were recovered, only one cercopith specimen (*Papio* sp.) is present in the faunal assemblage.

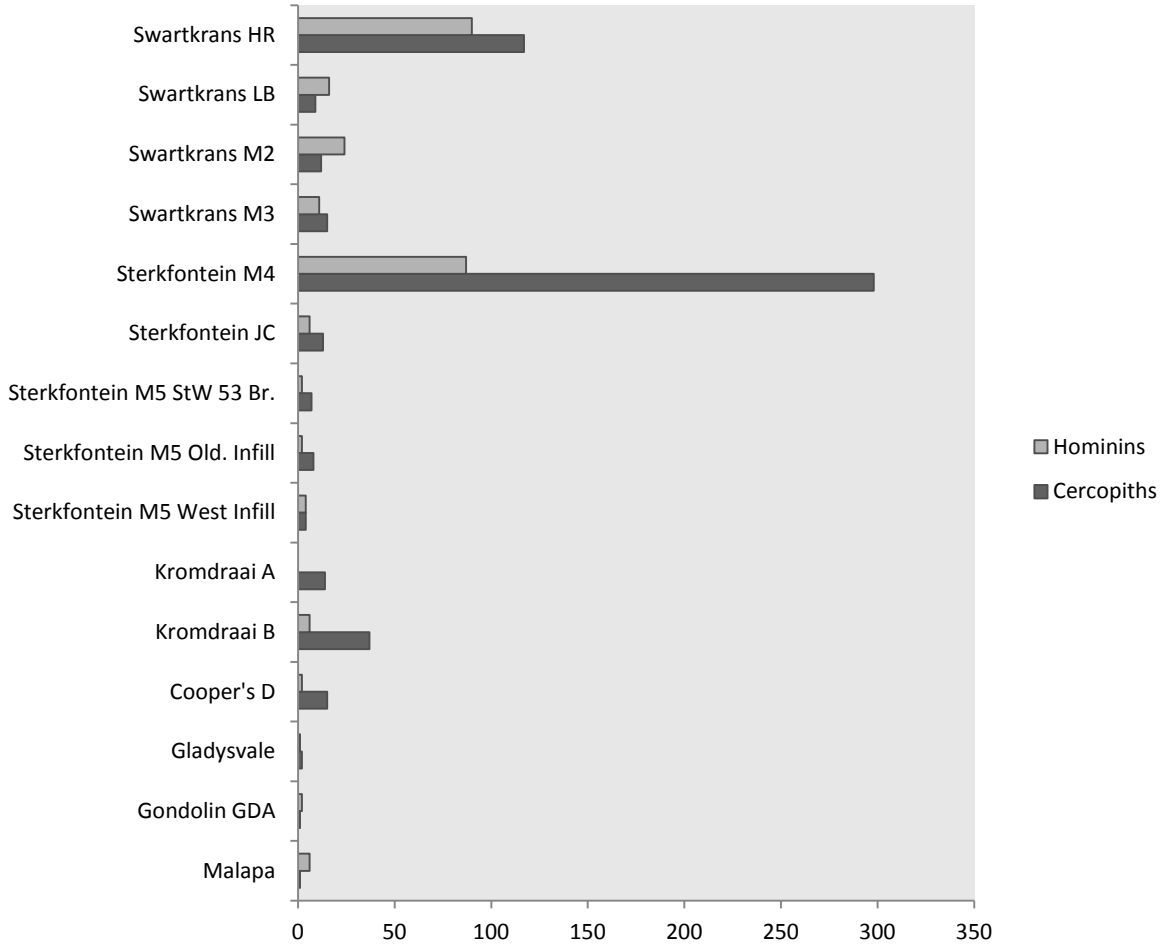



**Figure 9.2**. Abundance of hominin and non-hominin primates in Plio-Pleistocene fossil-bearing cave deposits from the Cradle of Humankind, in terms of minimum number of individuals (Br: Breccia; HR: Hanging Remnant, JC: Jacovec Cavern, LB: Lower Bank, M: Member, Old: Oldowan; StW: Sterkfontein).

## Hypotheses to explain the absence of non-hominin large primates at Malapa

The different modes of accumulation proposed for the faunal assemblage at Malapa (natural death trap and contribution by the brown hyaena) do not, in theory, exclude the presence of non-hominin primates and other early hominin taxa in the assemblage. Brown hyaenas are mostly scavengers (Lacruz and Maude, 2005; Skinner and Chimimba, 2005) and do not habitually include primates in their diet (Skinner and van Aarde, 1991; Skinner and Chimimba, 2005). They are, however, reported to become keen hunters of baboons and other large mammals when rearing cubs (Brain, 1981; Backwell *et*

*al*., 2009). I have argued the occupation of a part of the cave system as a breeding den by brown hyaenas, which potentially could be associated with the occurrence of some remains of cercopiths in the faunal assemblage. The natural death trap scenario, especially in the case of access to a cave by means of a vertical shaft, is said to be associated with an abundance of animals with good climbing skills, such as carnivores and primates (Pickering *et al*., 2004a; Clarke, 2007). For instance, the faunal assemblage associated with StW 573 from Sterkfontein Member 2 is composed of both australopithecine and other primate remains (Pickering *et al*., 2004a; see Table 9.2). It has been proposed that this assemblage accumulated mostly through a natural death trap, with a minor contribution by carnivores (Pickering *et al*., 2004a).

Here, different hypotheses are proposed to explain (1) the near-absence of large-bodied non-hominin primates in the faunal assemblage, and (2) the absence of other species of early hominins besides *Au. sediba*. Such hypotheses have implications regarding the ecology and behaviour of extinct primates, including hominins, and allow reflections on landscape occupation and interactions between hominin and non-hominin taxa, and between *Au. sediba* and other primates.

*Sample bias*

One possible way to explain the under-representation of papionins and the absence of other hominins in the assemblage is to attribute it to the small size of the sample or that the excavations to date have not reached areas where there will be higher levels of abundance of non-hominin primates. The co-occurrence of two early hominin taxa is only present in very large faunal assemblages (i.e. Swartkrans Members 1-2 and Sterkfontein Member 4). The absence of another hominin taxon at Malapa could therefore be explained by the small sample of the primate sub-assemblage. However, concerning the non-hominin primates, the Malapa faunal assemblage is similar to or larger than other deposits (e.g. Kromdraai A, Gladysvale, Jacovec Cavern and Member 5 StW 53

Breccia at Sterkfontein), where remains of cercopiths have been recovered (Broom and Robinson, 1949; Brain, 1981; Pickering, 1999; Kibii, 2007; Lacruz *et al.*, 2002). Furthermore, the faunal diversity at Malapa is high, with 27 species identified (see Tables 6.1 and 6.2 in Chapter 6). It seems very unlikely that the over-representation of hominin compared to non-hominin primates can only be a consequence of the relatively small size of the sample. Future excavations of *in situ* sediments and preparation of *ex situ* blocks should reveal whether or not fossil cercopiths are present at the site.

Finally, only MH1 and MH2 have been fully studied and analyzed from a morphological and taxonomic point of view (Berger *et al*., 2010; Carlson *et al*., 2011, Kibii *et al*., 2011; Zipfel *et al*., 2011; Berger, 2012). The other hominins (MH3-MH6) have been preliminarily assigned to *Au. sediba,* but a more definitive taxonomic attribution can only be made once the material has been studied.

*Morphology of the cave*

Another possible explanation for the absence of papionins and other hominins in the assemblage is that the morphology of the Malapa cave 1.977 Ma years ago was not suitable for these taxa. Modern baboons, geladas and chimpanzees have been reported to use caves and cliffs at night for various reasons, including protection against predators, geophagy (i.e. consumption of nutrients found in the soil of the cave), and thermoregulation (Altmann and Altmann, 1970; Gow, 1973; Busse, 1980; Brain, 1981; Iwamoto and Dunbar, 1983; Colishaw, 1994; Barrett *et al*., 2004; Pruetz, 2007). A recent study conducted on chacma baboons in the De Hoop Nature Reserve (Western Cape, South Africa) by Barrett and colleagues (2004) demonstrates that the primates were making regular use of the cave system at night, and of the vicinity of the cave during the day. The cave is located in a limestone area and the entrance consists of a narrow, vertical shaft opening out to the level ground. That vertical shaft is about 5 metre deep and leads to a horizontal tunnel, which opens to an underground cavern (Barrett *et al*., 2004). In the

absence of information regarding the ancient morphology of the cave and cave entry at Malapa, it is hard to discuss whether or not it was suitable for extinct baboons and geladas. The Malapa cave, located in a dolomitic area, probably offered a similar morphology as the cave used by the baboons in Barrett and colleagues's study. Furthermore, if the absence of non-hominin primates was due to the morphology of the cave, that would indicate that the Malapa cave was very different from neighbouring caves, which have yielded abundant remains of papionins, such as Sterkfontein, Swartkrans, Kromdraai, Gladysvale and Cooper's D (Table 9. 3 and Figure 9.7). Even though the primates recovered in these deposits were brought in for some of them by carnivores (Brain, 1981, 1993; Pickering and Carlson, 2002; Carlson and Pickering, 2003; Pickering *et al*., 2004b, 2004c; de Ruiter *et al*., 2009). It has also been suggested that they would sometimes occupy the cave ("sleeping-site hypothesis"; Brain, 1981, 1993; Pickering *et al*., 2004a; Val *et al*., submitted). The same argument applies to other hominin taxa, such as *A. africanus* and *P. robustus*, whose remains have been recovered in these cave deposits and for which the sleeping-site scenario has also been proposed (Brain, 1981, 1993).

Having considered the evidence, I do not believe that a specific morphology of the cave at Malapa is a sufficient or strong enough argument to explain the absence of other hominin taxa, and the under-representation of papionins in the assemblage.

*Palaeoenvironmental factors*

The potential role played by palaeoenvironment and palaeohabitat conditions around the Malapa site at 1.977 Ma to explain the absence of non-hominin primates in the assemblage is discussed here. The presence of taxa in the faunal spectrum associated with woodland savannah (i.e. *Tragelaphus strepsiceros* and *Tragelaphus scriptus;* Skinner and Chimimba, 2005) suggests a woody, as well as a riverine component (e.g. gallery forest) in the vicinity of the cave. Preliminary palaeoenvironmental reconstructions based on pollen and wood fragments extracted from a coprolite indicate the presence of moist forest

vegetation, composed of conifers, such as *Podocarpus/Afrocarpus* (Bamford *et al*., 2010). Analysis of plant phytoliths extracted from dental calculus, combined with stable carbon isotope and dental microwear texture studies reveal that *Au. sediba* had an almost exclusively $C_3$-based diet, which included tree leaves, bark, wood, fruits, grasses and sedges (Henry *et al*., 2012).

Modern baboons typically occupy woodland savannahs (Skinner and Chimimba, 2005). The extant southern African chacma baboons, *Papio hamadryas ursinus*, are generally associated with woodland savannahs and also found in less typical habitats, such as the montane uplands of the Drakensberg, or the riverine belts of the Namib Desert (Skinner and Chimimba, 2005). Extant gelada baboons, *Theropithecus gelada*, live in the high grasslands of the Ethiopian plateau in East Africa; these montane grasslands are characterised by scattered trees and bushes, and are cooler and less arid than the lowland areas (Iwamoto and Dunbar, 1983). Extinct species of cercopiths have been associated with different types of habitats, based on the reconstruction of their diets. *Papio hamadryas robinsoni, Papio (Dinopithecus) ingens* and *Parapapio* are regarded as mix-feeders to browsers with a $C_3$-based diet (frugivorous) (Lee-Thorp *et al*., 1989; Codron *et al*., 2005), consistent with a closed and woody environment. *Theropithecus oswaldi* is regarded as a mix-feeder to grazer with a predominant percentage of $C_4$ food (graminivorous), combined with some $C_3$-based food, such as fruits (Lee-Thorp *et al*., 1989; Codron *et al*., 2005), consistent with a more open environment. Other hominin taxa are associated with various habitats, also based on their diet. Isotopic and Sr/Ca studies demonstrated that *A. africanus* was a mix-feeder, with a $C_3$-based (fruits and leaves) diet, but with a significant $C_4$ component, including grasses, sedges and animals eating these plants, suggesting opportunistic food habits and the exploitation of relatively open environments, such as woodlands and grasslands (Sponheimer and Lee-Thorp, 1999; van der Merwe *et al*., 2003; Sponheimer *et al*., 2005a, 2005b). Recent studies show that *P. robustus* has an abundance profile similar to woodland adapted species (de Ruiter *et al*., 2008). However, isotopic and Sr/Ca analyses demonstrate that the diet of *P. robustus* is

variable, and included both $C_4$ grassland and $C_3$ woodland foods, indicative of a species with a non-specialized diet that can include woodland food such as seeds, fruits and underground resources, as well as savannah foods such as grasses, sedges or animals that consumed these foods (Sillen, 1992; Sillen *et al*., 1995; Lee-Thorp *et al*., 1994; Sponheimer *et al*., 2005a, 2005b, 2006). Sr/Ca and dental topography analysis suggest that early *Homo* had a diverse diet, including tough and flexible food, such as meat and other animal soft tissues (Ungar, 2004; Teaford *et al*., 2002; Ungar *et al*., 2006), as well as vegetal and underground resources, such as plants, tubers, bulbs and/or possibly animals eating these undergrounds resources (Sillen *et al*., 1995; Teaford *et al*., 2002; Ungar *et al*., 2006).

The variety of habitats and food requirements of non-hominin primates and other early hominin taxa suggests that the type of vegetation present around the Malapa cave would have attracted at least some of the primates (e.g. papionins, if the vicinity of the cave offered a good tree coverage and fruits and leaves, which are an important component of the diet of these this taxon). Furthermore, the palaeoenvironment of Malapa does not seem to differ from sites that have yielded significant numbers of non-hominin primates, gracile and robust australopithecines, and early *Homo*, such as Sterkfontein Member 4, Swartkrans Members 1-3, Kromdraai, Cooper's D and Gladysvale. For these sites, a mosaic of environments has been proposed, including open grasslands, woody and riverine components (Vrba, 1975, 1980; Avery, 2001; de Ruiter *et al*., 2009; Steininger, 2010).

I argue that there is no strong evidence to support the hypothesis that differences in palaeoenvironment would explain the absence of non-hominin primates and other hominin taxa in the Malapa faunal assemblage.

*Competition with other primates*

Another hypothesis considers the primate sub-assemblage as a representative sample, with an extremely high number of hominins, all belonging to *Au. sediba*, a very

low representation of cercopiths, and the absence of other hominin taxa. Behavioural and ecological factors are invoked to explain this pattern. A natural death trap scenario, combined with a sleeping site scenario, whereby the hominins used the cave as a shelter, could imply an exclusive use of the cave by one species of primate taxon, namely, in the case of Malapa, *Au. sediba*. The sleeping site scenario, usually associated with predation inside the cave by carnivores, has been mentioned by several authors to explain the abundance of primates in some Plio-Pleistocene deposits, for instance at Swartkrans Member 1, Lower Bank and Hanging Remnant (Brain, 1981, 1993) and at Cooper's D (Val *et al*., submitted).

Modern primates, such as baboons and chimpanzees, frequent caves to access water or soil nutrients and to regulate their body temperature (Barrett *et al*., 2004; Pruetz, 2007), or to seek protection against predators at night (Simons, 1966; Altmann and Altmann, 1970; Grobler and Wilson, 1972; Gow, 1973; Busse, 1980; Brain, 1981; Cowlishaw, 1994; Hart, 2000; Mc Grew *et al*., 2003). The Malapa cave system could have provided such shelter. Studies on modern baboons and geladas show a tendency to territoriality, whereby groups naturally tend to avoid contact with each other (Jay, 1965; Bates, 1970). Specific areas such as a water hole, a sleeping site, or a food resource, are in most cases exclusive to a particular primate group (DeVore, 1963; Jay, 1965; Jewell, 1966; Mason, 1968). It is not unreasonable to suggest that the same could apply to australopithecines, and therefore that the Malapa cave was exclusively used by a group of *Au. sediba* at one given time, associated with the moment of accumulation of MH1 and MH2, and on alternate occasions by other groups of primates. In other words, because of territoriality and competition between primates, when one group would occupy the cave, the others hominin and non-hominin taxa would avoid the area, and therefore not be represented in the deposit.

# General conclusion

An innovative *palaeoforensic taphonomic* approach, combining palaeontological and physical analyses with a 3D spatial study and a virtual reconstruction of the original burial position of the hominins, was used to address taphonomic questions relating to the accumulation, burial and fossilisation processes of the two well-preserved *Au. sediba* individuals (MH1 and MH2), from early Pleistocene deposits at the Malapa cave. The taphonomic study of the hominins and associated fauna highlights the presence of several characteristics, indicating that the cave served as a death trap. Evidence of carnivore activity is low, but the occurrence in the assemblage of a few deciduous teeth of brown hyaenas, carnivore coprolites and cylindrical shafts, could suggest the use by *P. brunnea* of an upper part of the cave system as a breeding den, which remains to be confirmed. Various lines of evidence in accordance with a natural death trap scenario were provided by the palaeontological and physical analyses of the faunal assemblage. The skeletal part representation follows a density-mediated pattern and does not show any indication of carnivore or water selection, and there is an abundance of complete and near complete bones, antimeric sets of fossils, as well as elements preserved in articulation. The physical approach highlighted the heterogeneity of the assemblage in terms of bone preservation. It illustrated the important role played by the cycles of calcification/decalcification in the degree of fossil preservation. Microscopic analysis of the bone surface revealed the very low impact of carnivore damage on the assemblage, and the absence of modifications caused by rodents, hominins and birds of prey. The only important biotic agents in terms of bone surface damage are insects, which seem to have modified the bones pre- and post-fossilisation. There is little evidence for sedimentary and water abrasion, challenging the idea of transport of bones in water.). The preliminary hypothesis suggesting transport of the hominin corpses from an upper part of the cave system to a lower part of the cave system by a debris flow (Dirks *et al*., 2010) is not validated by the results of this study. Rather, based on the available evidence, it seems more likely that the two hominins MH1

and MH2 have not been transported from their death site to their burial site (i.e. where they have been recovered). The little movement observed for some hominin bones most likely occurred after the burial, due to taphonomic processes that are yet to be identified (the possible role played by termites is the topic ongoing research).

In reconstructing the formation process for the fossil assemblage (i.e. taphonomic pathway), it appears that living animals accidentally fell through a vertical shaft opening, which led to a deep chamber in the cave system, one that was inaccessible to scavengers and rodents. Surface material from the surrounding landscape would have been introduced via the shaft by gravity and by heavy rain, and mixed within the talus cone created at the bottom of the vertical shaft with elements from the carnivore den in an upper chamber. The action of a debris flow in the transportation, accumulation, mixing and burial of the faunal assemblage is still under debate.

The spatial approach consisted of an innovative 3D analysis of the distribution of the remains inside the deposit and reconstruction of the burial position of the hominins. It required the creation of a 3D model of the cave, including virtual renderings of the hominin remains in their original *in situ* position. This involved the refitting of *ex situ* hominin material as a necessary preliminary step to the spatial analysis. The study of bone distribution and orientation inside the deposit showed very little dispersal, and therefore very little movement of the bones across the deposit. It made it possible to reconstruct the original position of the hominins at the time of final burial and preservation, with MH1 lying on his front, with his head on its left side and facing south, and his limbs along his body. MH2 was lying on her back, with her head towards the south, her arms along her body and her legs flexed, with the knees pointing to the east, and her left leg on top of the right one.

The results of the palaeoforensic taphonomic study of the hominins indicate that MH1 most likely entered the site prior to MH2. They both decomposed in a primary deposit, at the bottom of the vertical shaft, with no disruption by scavengers and very

little by insects. Mummification most likely took place before burial. Some post-burial movement took place inside the deposit after burial in coarse sand that slightly displaced the bones in various directions, but only for very short distances.

The mode of accumulation of most individuals - hominins and others - from the Malapa assemblage, via a natural death trap scenario with the limited involvement of carnivores and other biotic agents, and followed by a relatively quick burial and sedimentation, has important implications for future excavations of the *in situ* deposits, as well as for forthcoming palaeoecological and palaeoenvironmental interpretations. The taphonomic scenario proposed for MH1 and MH2 is that they entered the cave system as complete bodies and were most likely buried in a mummified state, which argues in favour of potential preservation of soft tissues. It also means that all the skeletal remains should be preserved in the deposit, either still *in situ*, in the unexcavated sediments, or in *ex situ* blocks of calcified sediments removed during mining and awaiting physical preparation. The reconstruction of the original burial position of the hominins allows the prediction of the location of the missing remains, which suggests that the holotype (MH1) and the paratype (MH2) of the newly described *Au. sediba* species will in due course be represented by complete skeletons.

## References

Abdala, F., Cisneros, J.C. and Smith, R.M.H. (2006) Faunal aggregation in the early Triassic Karoo Basin: earliest evidence of shelter-sharing behaviour among tetrapods? *PALAIOS*, vol.21, pp.507-512.

Adam, F., Boura, F. and Duday, H. (1992) La fouille de Saint-Rémy-la-Calonne: une opération d'archéologie funéraire expérimentale, ou l'anthropologie de terrain en quête de ses références, *Les Nouvelles de l'Archéologie*, vol.48-49, pp.59-61.

Adams, J.W. (2006) Taphonomy and Paleoecology of the Gondolin Plio-Pleistocene Cave Site, South Africa, Ph.D. thesis, Washington University.

Adams, J.W. (2012) Craniodental and postcranial remains of the extinct porcupine *Hystrix makapanensis* Greenwood, 1958 (Rodentia: Hystricidae) from Gondolin, South Africa, *Annals of the Ditsong National Museum of Natural History*, vol.2, pp.7-17.

Adams, J.W., Herries, A.I.R., Kuykendall, K.L. and Conroy, G.C. (2007a) Taphonomy of a South African cave: geological and hydrological influences on the GD 1 fossil assemblage at Gondolin, a Plio-Pleistocene paleocave system in the Northwest Province, South Africa, *Quaternary Science Reviews*, vol.26, pp.2526-2543.

Adams, J.W., Hemingway, J., Kegley, A.D.T. and Thackeray, J.F. (2007b) Luleche, a new paleontological site in the Cradle of Humankind, North-West Province, South Africa, *Journal of Human Evolution*, vol.53, pp.751-754.

Agenbroad, L. D. (1984) Mammoth trampling and other bone modifying processes at the Hot Springs Mammoth site, South Dakota, *Abstracts of the First International Conference on Bone Modification*, Carson City, Nevada, August 17-19, pp.1-2.

Alemseged, Z., Spoor, F., Kimbel, W.H., Bobe, R., Geraads, D., Reed, D. and Wynn, J.G. (2006) A juvenile early hominin skeleton from Dikika, Ethiopia, *Nature*, vol.443, pp.296-301.

Allison, T.A., Smith, C.R., Kukert, H., Deming, J.W. and Bennett, B.A. (1991) Deep-water taphonomy of vertebrate carcasses: a whale skeleton in the Bathyal Santa Catalina Basin, *Paleobiology*, vol.17, no.1, pp.78-89.

Altmann, S. and Altmann, J. (1970*) Baboon Ecology*. New York: S Karger.

Amendt, J., Krettek, R. and Zehner, R. (2004) Forensic entomology, *Naturwissenschaften*, vol.91, pp.51-65.

Anderson, G.S. (2010) Factors that influence insect succession on carrion, In: Byrd, J.H. and Castner, J.L. (eds.) *Forensic Entomology, The Utility of Arthropods in Legal Investigation*, CRC Press: Taylor and Francis Group.

Andrews, P. (1990) *Owls, Caves and Fossils*. University of Chicago Press: Chicago.

Andrews, P. and Cook, J. (1985) Natural modifications to bones in a temperate setting, *Man*, vol.20, no.4, pp.675-691.

Andrews, P. and Fernández-Jalvo, Y. (1997) Surface modifications of the Sima de los Huesos fossil humans, *Journal of Human Evolution*, vol.33, pp.191-217.

Arbogast, R.-M. (1995) Les restes du chien de la structure 561 (sect. E): Rapport préliminaire d'étude archéozoologique, In: Mission archéologique de la vallée du Strymon, Fouilles néolithiques franco-bulgares de Kovacevo. Rapport no.9, campagne de 1994, pp.60-62. Centre de Recherches Protohistoriques, Université de Paris I-Panthéon-Sorbonne, Paris (unpublished).

Archer, M.S. and Elgar, M.A. (1998) Cannibalism and delayed pupation in hide beetles, *Dermestes maculatus* DeGeer (Coleoptera: Dermestidae), *Australian Journal of Entomology*, vol.37, pp.158-161.

Armour-Chelu, M. and Andrews, P. (1994) Some effects of bioturbation by earthworms (*Oligochaeta*) on archaeological sites, *Journal of Archaeological Science*, vol.21, pp.433-443.

Backwell L.R. and d'Errico F. (2001) First evidence of termite-foraging by Swartkrans early hominids, *PNAS,* vol.98, no.4, pp.1358-1363.

Backwell, L.R. and d'Errico, F. (2003) Additional evidence on the early hominid bone tools from Swartkrans with reference to spatial distribution of lithic and organic artefacts, *South African Journal of Science*, vol.99, pp.259-267.

Backwell, L.R. and d'Errico, F. (2008) Early hominid bone tools from Drimolen, South Africa, *Journal of Archaeological Science*, vol.35, pp.2880-2894.

Backwell, L.R., Pickering, R., Brothwell, D., Berger, L.R., Witcomb, M., Martill, D., Penkman, K. and Wilson, A. (2009) Probable human hair found in a fossil hyaena coprolite from Gladysvale cave, South Africa, *Journal of Archaeological Science*, vol.36, no.6, pp.1269-1276.

Backwell, L.R., Parkinson, A.H., Roberts, M., d'Errico, F. and Huchet, J.-B. (2012) Criteria for identifying bone modification by termites in the fossil record, *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol.337-338, pp.72-87.

Bader, K.S. (2003) Insect Trace Fossils on Dinosaur Bones from the Upper Jurassic Morrison Formation, Northeastern Wyoming, and their Use in Vertebrate Taphonomy, M.Sc. thesis, University of Kansas.

Bader, K.S., Hasiotis, S.T. and Martin, L.D. (2009) Application of forensic science techniques to trace fossils on dinosaur bones from a quarry in the Upper Jurassic Morrison Formation, Northeastern Wyoming, *PALAIOS*, vol.24, pp.140-158.

Bamford, M.K., Neumann, F.H., Pereira, L.M., Scott, L., Dirks, P.H.G.M. and Berger, L.R. (2010) Botanical remains from a coprolite from the Pleistocene hominin site of Malapa, Sterkfontein Valley, South Africa, *Palaeontologia Africana*, vol.45, pp.23-28.

Barrett, L., Gaynor, D., Rendall, D., Mitchell, D. and Henzi, S.P. (2004) Habitual cave use and thermoregulation in chacma baboons (*Papio hamadryas ursinus*), *Journal of Human Evolution*, vol.46, pp.215-222.

Bates, B.C. (1970) Territorial behavior in pimates: a review of recent field studies, *Primates*, vol.11, pp.271-284.

Baxter, P.J. (1990) Medical effects of volcanic eruptions, *Bulletin of Volcanology*, vol.52, pp.535-544.

Beary, M.O. and Lyman, R.L. (2012) The use of taphonomy in forensic anthropology: past trends and future prospects, In: Dirkmaat, D.C. (ed.) *A Companion to Forensic Anthropology, First Edition*, Backwell Publishing Ltd. Chapter 25, pp.499-527.

Bedford, P.J. and Tsokos, M. (2012) The occurrence of cadaveric spasm is a myth, *Forensic Science, Medicine, and Pathology*, DOI 10.1007/s12024-012-9391-5.

Behrensmeyer, A.K. (1975) The taphonomy and paleoecology of Plio-Pleistocene vertebrate assemblages East of Lake Rudolf, Kenya, *Museum Comparative Zoological Bulletin*, vol.146, pp.473-578.

Behrensmeyer, A.K. (1978) Taphonomic and ecologic information from bone weathering, *Paleobiology*, vol.4, no.2, pp.150-162.

Behrensmeyer, A.K. (1982) Time resolution in fluvial vertebrate assemblages, *Paleobiology*, vol.8, no.3, pp.211-227.

Behrensmeyer, A.K. (1988) Vertebrate preservation in fluvial channels, *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol.63, pp.183-199.

Behrensmeyer, A.K., Gordon, K.D. and Yanagi, G.T. (1986) Trampling as a cause of bone surface damage and pseudo-cutmarks, *Nature*, vol.319, pp.768-771.

Behrensmeyer, A.K., Damuth, J.D., DiMichele, W.A., Potts, R., Sues, H.-D. and Wing, S.L. (eds.) (1992) *Terrestrial Ecosystems Through Time*. The University of Chicago Press: Chicago.

Belfer-Cohen, A. and Hovers, E. (1992) In the eye of the beholder: Mousterian and Natufian burials in the Levant, *Current Anthropology*, vol.33, no.4, pp.463-471.

Berger, L.R. (2006) Brief Communication: Predatory bird damage to the Taung type-skull of *Australopithecus africanus* Dart 1925, *American Journal of Physical Anthropology*, vol.131, pp.166-168.

Berger, L.R. (2012) *Australopithecus sediba* and the earliest origins of the genus *Homo*, *Journal of Anthropological Sciences*, vol.90, pp.1-16.

Berger, L.R. and Tobias, P.V. (1994) New discoveries at the early hominid site of Gladysvale, South Africa, *South African Journal of Science*, vol.90, pp.223-226.

Berger, L.R. and Clarke, R.J. (1995) Eagle involvement in accumulation of the Taung child fauna, *Journal of Human Evolution*, vol.29, pp.275-299.

Berger, L.R. and Lacruz, R. (2003) Preliminary report on the first excavations at the new fossil site of Motsetse, Gauteng, South Africa, *South African Journal of Science*, vol.99, pp.279-282.

Berger, L.R. and McGraw, W.S. (2007) Further evidence for eagle predation of, and feeding damage on, the Taung child, *South African Journal of Science*, vol.103, pp.496-498.

Berger, L.R., Keyser, A.W. and Tobias, P.V. (1993) Brief Communication: Gladysvale: first early hominid site discovered in South Africa since 1948, *American Journal of Physical Anthropology*, vol.92, pp.107-111.

Berger, L.R., de Ruiter, D.J., Steininger, C.M. and Hancox, J. (2003) Preliminary results of excavations at the newly investigated Coopers D deposit, Gauteng, South Africa, *South African Journal of Science*, vol.99, pp.276-278.

Berger, L.R., Pickering, R., Kuhn, B., Backwell, L., Hancox, P.J., Kramers, J.D. and Boshoff, P. (2009) A Mid-Pleistocene *in situ* fossil brown hyaena (*Parahyaena brunnea*) latrine from Gladysvale Cave, South Africa, *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol.279, pp.131-136.

Berger, L. R., de Ruiter, D.J., Churchill, S.E., Schmid, P., Carlson, K.J., Dirks, P.H.G.M. and Kibii, J.M. (2010) *Australopithecus sediba*, a new species of *Homo*-like Australopith from South Africa, *Science*, vol.328, pp.195-204.

Berna, F., Goldberg, P., Horwitz, L.K., Brink, J., Bamford, M. and Chazan, M. (2012) Microstratigraphic evidence of *in situ* fire in the Acheulean strata of Wonderwerk Cave, Northern Cape Province, South Africa, *PNAS*, vol.109, no.20, pp.1215-1220.

Binford, S. R. (1968) A structural comparison of disposal of the dead in the Mousterian and the Upper Paleolithic, *Southwestern Journal of Anthropology*, vol.24, no.2, pp.139-154.

Binford, L.R. (1978) *Nunamiut Ethnoarchaeology*. New York: Academic Press (Studies in Archaeology).

Binford, L.R. (1981) *Bones, Ancient Men and Modern Myths*. Academic Press: New York.

Binford, L. R. and Bertram, J. B. (1977) Bone frequencies and attritional processes, In: Binford, L.R. (ed.) *For Theory Building in Archaeology*. New York: Academic Press, pp. 77-153.

Binford, L.R., Mills, M.G.L. and Stone, N.M. (1988) Hyaena scavenging behavior and its implications for interpretation of faunal assemblages from FLK22 (the Zinj Floor) at Olduvai Gorge, *Journal* of *Anthropological Archaeology,* vol.7, pp.99-135.

Blatt, H., Tracy, J.R. and Owens, B. (2006) *Petrology: Igneous, Sedimentary and Metamorphic*. Freeman: New York, ed.3.

Blumenschine, R.J. (1988) An experimental model of the timing of hominid and carnivore influence on archaeological bone assemblages, *Journal of Archaeological Science*, vol.15, pp.483-502.

Blumenschine, R.J. (1995) Percussion marks, tooth marks, and experimental determinations of the timing of hominid and carnivores access to long bones at FLK Zinjanthropus, Olduvai Gorge, Tanzania, *Journal of Human Evolution*, vol.29, pp.21-51.

Blumenschine, R.J. and Selvaggio, M.M. (1991) On the marks of marrow bone processing by hammerstones and hyaenas: their anatomical patterning and archaeological implications, In: Clark, J.D. (ed.) *Cultural Beginnings - Approaches to Understanding Early Hominid Life-ways in the African Savanna*, UISPP, Mainz, pp.17-32.

Boaz, N.T. and Behrensmeyer, A.K. (1976) Hominid taphonomy: transport of human skeletal parts in an artificial fluviatile environment, *American Journal of Physical Anthropology*, vol.45, pp.53-60.

Boaz, D.D. (1994) Taphonomy and the fluvial environment. Examples from Pliocene deposits of the Shunguran Formation, Omo Basin, Ethiopia, In: Corruccini, R.S., and

Ciochon, R.L. (eds.) *Integrative Paths of the Past. Paleoanthropological advances in Honor of F. Clark Howell*. Englewood Cliffs, New Jersey, Chapter 19, pp.377-414.

Boesch, C. and Boesch, H. (1989) Hunting behavior of wild chimpanzees in the Tai National Park, *American Journal of Physical Anthropology*, vol.78, pp.547-573.

Boesch, C. and Boesch-Achermann, H. (2000) *The Chimpanzees of the Taï Forest. Behavioral Ecology and Evolution*. Oxford University Press.

Boesch, C., Crockford, C., Herbinger, I., Wittig, R., Moebius, Y. and Normand, E. (2008) Intergroup conflicts among chimpanzees in Taï National Park: lethal violence and the female perspective, *American Journal of Primatology*, vol.70, pp.519-532.

Bolter, D.R. and Zihlman, A.L. (2012) Skeletal development in *Pan paniscus* with comparisons to *Pan troglodytes*, *American Journal of Physical Anthropology*, vol.147, pp.629-636.

Bonnichsen R. (1973) Some operational aspects of human and animal bone alteration, In: Gilbert B.M. (ed.) *Mammalian Osteoarchaeology*. North America, Missouri Archaeological Society: Columbia; pp.9-24.

Bonnichsen, R. and Will, R.T. (1980) Cultural modification of bone: the experimental approach in faunal analysis, In: Gilbert, B.M., (ed.) *Mammalian Osteology*. Laramie, Wyoming: B. Miles Gilbert Publisher, pp.7-30.

Bornemissza, G.F. (1957) An analysis of arthropod succession in carrion and the effect of its decomposition on the soil fauna, *Australian Journal of Zoology*, vol.5, no.1, pp.1-12.

Botha-Brink, J. and Modesto, S.P. (2007) A mixed-age classed 'pelycosaur' aggregation from South Africa: earliest evidence of parental care in amniotes? *Proceedings of the Royal Society of London*, vol.274, pp.2829-2834.

Bountalis, A. (2011) Cave Usage and the Implications of Multiple Taphonomic Agents on a Faunal Assemblage, M.Sc. thesis, University of the Witwatersrand, Johannesburg.

Bouyssonie, J. (1954) Les sépultures moustériennes, *Quaternaria*, vol.1, pp.107-115.

Braga, J. and Thackeray, J.F. (2003) Early *Homo* at Kromdraai B: probabilistic and morphological analysis of the lower dentition, *Comptes Rendus Palevol*, vol.2, pp.269-279.

Brain, C.K. (1958) *The Transvaal Ape-Man-Bearing Cave Deposits*, Transvaal Museum Memoirs, no.11.

Brain, C.K. (1967) Bone weathering and the problem of pseudotools, *South African Journal of Science*, vol.32, pp.1-11.

Brain, C.K. (1969) The contribution of Namib desert Hottentots to an understanding of australopithecine bone accumulations, *Scientific Papers of the Namib Desert Research Station*, vol.39, pp.13-22.

Brain C.K. (1973) An interpretation of the bone assemblage from the Kromdraai australopithecine site, South Africa, In: Tuttle, R. (ed.) *Paleoanthropology, Morphology and Ecology*. The Hague: Mouton, pp.225-243.

Brain, C.K. (1974) Some suggested procedures in the analysis of bone accumulations from southern African Quaternary sites, *Annals of the Transvaal Museum*, vol.29, no.1, pp.1-8.

Brain, C.K. (1975) An introduction to the South African australopithecine bone accumulations, In: Clason, A.T. (ed.) *Archaeological Studies*, pp.109-119.

Brain, C.K. (1976) Some principles in the interpretation of bone accumulations associated with Man, In: Isaac, G.L. and McCown, E.R. (eds.) *Human Origins: Louis Leakey and the East African Evidence*, pp.97-116. W. A. Benjamin, Menlo Park: California.

Brain, C.K. (1981) *The Hunters or the Hunted? Introduction to African Cave Taphonomy*. The University of Chicago Press: Chicago.

Brain, C.K. (1993) *Swartkrans, A Cave's Chronicle of Early Man*. Brain, C.K. (ed.) Transvaal Museum Monograph No.8: Pretoria.

Brain, C.K. and Sillen, A. (1988) Evidence from the Swartkrans cave for the earliest use of fire, *Nature*, vol.336, pp.464–466.

Brain, C.K. and Shipman, P. (1993) The Swartkrans bone tools, In: Brain, C.K., ed. *Swartkrans, A Cave's Chronical of Early Man*, pp.195-216. Transvaal Museum Monograph No.8: Pretoria.

Britt, B.B., Scheetz, R.D. and Dangerfield, A. (2008) A suite of dermestid beetle traces on dinosaur bone from the Upper Jurassic Morrison Formation, Wyoming, USA, *Ichnos: An International Journal for Plant and Animal Traces*, vol.15, no.2, pp.59-71.

Broom, R. (1936) New fossil anthropoid skull from South Africa, *Nature*, vol.138, pp.486-488.

Broom, R. (1938) The Pleistocene Anthropoid Apes of South Africa, *Nature*, vol.142, pp.377-379.

Broom, R. (1947) Discovery of a new skull of the South African ape-man, *Plesianthropus*, *Nature,* vol. 159, pp.672.

Broom, R. and Robinson, J.T. (1949) A new type of fossil baboon, *Gorgopithecus major*, *Proceedings of the Zoological Society of London*, vol.119, no.2, pp.379-386.

Brophy, J.K. (2004) Preliminary Report on the Faunal Remains and Taphonomic Analysis of Plover's Lake Cave, Cradle of Humankind, South Africa, Ph.D. thesis, University of Tennessee, Knoxville.

Brown, F.H. (1982) Tulu Bor Tuff at Koobi Fora correlated with the Sidi Hakoma Tuff at Hadar, *Nature*, vol.300, pp.631-633.

Brown, F. H. and McDougall, I. (1993) Chapter 2, geologic setting and age, In: Walker, A. and Leakey, R. (eds.) *The Nariokotome* Homo erectus *Skeleton*, pp.2-20.

Brugal J-P, Fosse P. and Guadelli J-L. (1997) Comparative study of bone assemblages made by recent and Pleistocene hyenids, In: Hannus L.A., Rossum L. and Winham R.P. (eds.) *Proceedings of the 1993 Bone Modification Conference, Hot Springs, South Dakota*, Occasional Publication no.1, Archaeology Laboratory, Augusta College: Sioux Falls, SD, pp.158-187.

Brunet, M., Guy, F., Pilbeam, D., Mackaye, H.T., Likius, A., Ahounta, D., Beauvilain, A., Blondel, C., Bocherens, H., Boisserie, J.-R., de Bonis, L., Coppens, Y., Dejax, J., Denys, C., Duringer, P., Eisenmann, V., Fanone, G., Fronty, P., Geraads, D., Lehmann, T., Lihoreau, F., Louchart, A., Mahamat, A., Merceron, G., Mouchelin, G., Otero, O., Campomanes, P.P., Ponce de León, M., Rage, J.-C., Sapanet, M., Schuster, M., Sudre, J., Tassy, P., Valentin, X., Vignaud, P., Viriot, L., Zazzo, A. and Zollikofer, C. (2002) A new hominid from the Upper Miocene of Chad, Central Africa, *Nature*, vol.418, pp.145-151.

Bunn, H.T. (1981a) Archaeological evidence for meat-eating by Plio-Pleistocene hominids from Koobi Fora and Olduvai Gorge, *Nature*, vol.291, pp.574-577.

Bunn, H.T. (1981b) A note on a comparative study of bone assemblages accumulated by carnivores and by Basarwa Hunter Gatherers, *Botswana Notes and Record*, vol.13, p.151.

Bunn, H.T. (1982) Meat-Eating and Human Evolution: Studies on the Diet and Subsistence Patterns of Plio-Pleistocene Hominids in East Africa, Ph.D. thesis, University of California, Berkeley.

Bunn, H. T. (1983) Comparative analysis of modern bone assemblages from a San hunter-gatherer camp in the Kalahari desert, Botswana, and from a spotted hyaena den near Nairobi, Kenya, In: Clutton-Brock, J. and Grigson, C. (eds.) *Animals and Archaeology: I. Hunters and Their Prey*. British Archaeological Reports International Series, pp.143-148: Oxford.

Bunn, H.T., Kroll, E.M., Ambrose, S.H., Behrensmeyer, A.K., Binford, L.R., Blumenschine, R.J., Klein, R.G., McHenry, H.M., O'Brien, C.J. and Wymer, J.J. (1986) Systematic butchery by Plio-Pleistocene hominids at Olduvai Gorge, Tanzania, *Current Anthropology*, vol. 27, pp.431-452.

Busse, C. (1980) Leopard and lion predation upon chacma baboons living in the Moremi Wildlife Reserve, *Botswana Notes and Records*, vol.12, pp.15-21.

Byrd, J.H. and Castner, J.L. eds (2010) *Forensic Entomology, The Utility of Arthropods in Legal Investigation*, CRC Press: Taylor and Francis Group.

Campmas, E. and Beauval, C. (2008) Consommation osseuse des carnivores: résultats de l'étude de l'exploitation de carcasses de bœuf (*Bos taurus*) par des loups captifs, *Annales de Paléontologie*, vol.94, pp.167-186.

Campobasso, C.P., Falamingo, R., Grattagliano, I. and Vinci, F. (2009) The mummified corpse in a domestic setting, *American Journal of Forensic Medicine and Pathology*, vol.30, pp.307-310.

Capaldo, S.D. (1995) Inferring Hominid and Carnivore Behavior from Dual-Patterned Archaeofaunal Assemblages, Ph.D. thesis, Rutgers University.

Capaldo, S.D. (1997) Experimental determinations of carcass processing by Plio-Pleistocene hominids and carnivores at FLK 22 (*Zinjanthropus*), Olduvai Gorge, Tanzania, *Journal of Human Evolution*, vol.33, pp.555-597.

Capaldo, S.D. and Blumenschine, R.J. (1994) A quantitative diagnosis of notches made by hammerstone percussion and carnivore gnawing on bovid long bones, *American Antiquity*, vol.59, no.4., pp.724-748.

Capaldo, S.D. and Peters, C.R. (1995) Skeletal inventories from wildebeest drowning at Lakes Masek and Ndutu in the Serengeti ecosystem of Tanzania, *Journal of Archaeological Science*, vol.22, no.3, pp.385-408.

Carlson, K.J. and Pickering, T.R. (2003) Intrinsic qualities of primate bones as predictors of skeletal element representation in modern and fossil carnivore feeding assemblages, *Journal of Human Evolution*, vol.44, pp.431-450.

Carlson, K.J., Stout, D., Jashashvili, T., de Ruiter, D.J., Tafforeau, P., Carlson, K. and Berger, L.R. (2011) The endocast of MH1, *Australopithecus sediba*, *Science*, vol.333, pp.1402-1407.

Castel, J.-C. (1999) Le rôle des petits carnivores dans la constitution et l'évolution des ensembles archéologiques du Paléolithique supérieur. L'exemple du Solutréen de Combe Saunière, Dordogne, France, *Anthropozoologica*, vol.29, pp.33-54.

Chalmin, E., d'Orlyé, F., Zinger, L., Charlet, L., Geremia, R.A., Orial, G., Menu, M., Baffier, D. and Reiche, I. (2007) Biotic versus abiotic calcite formation on prehistoric cave paintings: the Arcy-sur-Cure 'Grande Grotte' (Yonne, France) case, *Geological Society, London, Special Publications*, vol.279, pp.185-197.

Clark, J.D. (1993) Stone artefact assemblages from Members 1-3, Swartkrans Cave, In: Brain, C.K., (ed.) *Swartkrans, A Cave Chronicle's of Early Man*, pp.167-194. Transvaal Museum Monograph No.8, Pretoria.

Clark, M.A., Worrell, M.B. and Pless, J.E. (1997) Postmortem changes in soft tissue, In: Haglund, W.D. and Sorg, M.H. (eds.) *Forensic Taphonomy: The Postmortem Fate of Human Remains*, pp.151-170. CRC Press, Boca Raton, FL: USA.

Clarke, R.J. (1985) *Australopithecus* and early *Homo* in southern Africa, In: Delson, E. (ed.) *Ancestors: the Hard Evidence*, pp.171-177. Alan R. Liss: New York.

Clarke, R.J. (1986) Early Acheulean with *Homo habilis* at Sterkfontein, In: Tobias, P.V. (ed.) *Hominid Evolution: Past, Present, and Future*, pp.287-298. Alan R. Liss: New York

Clarke, R.J. (1988) A new *Australopithecus* cranium from Sterkfontein and its bearing on the ancestry of *Paranthropus,* In: Grine, F. (ed.) *Evolutionary History of the 'Robust' Australopithecines*, pp.285-292. Aldine de Gruyter: New York.

Clarke, R.J. (1998) The first ever discovery of a well-preserved skull and associated skeleton of *Australopithecus*, *South African Journal of Science*, vol.94, pp.460-463.

Clarke, R.J. (1999) Discovery of complete arm and hand of the 3.3 million-year-old *Australopithecus*, *South African Journal of Science*, vol.95, pp.477-480.

Clarke, R.J. (2007) Taphonomy of Sterkfontein *Australopithecus* skeletons, In: Pickering, T.R., Schick, K. and Toth, N. (eds.) *Breathing Life into Fossils: Taphonomic Studies in Honor of C.K. (Bob) Brain*, pp. 199-205. Bloomington (Indiana): Stone Age Institute Press.

Clarke, R.J. (2008) Latest information on Sterkfontein's *Australopithecus* skeleton and a new look at *Australopithecus*, *South African Journal of Science*, vol.104, pp.443-449.

Clarke, R.J. (2012) A brief review of history and results of 40 years of Sterkfontein excavations, In: Reynolds, S.C. and Gallagher, A. (eds.) *African Genesis, Perspectives on Hominin Evolution*, pp.120-141. Cambridge University Press.

Coard, R. and Dennell, R.W. (1995) Taphonomy of some articulated skeletal remains: transport potential in an artificial environment, *Journal of Archaeological Science*, vol.22, pp.441-448.

Coard, R. (1999) One bone, two bones, wet bones, dry bones: transport potentials under experimental conditions, *Journal of Archaeological Science*, vol.26, pp.1369-1375.

Codron, D., Luyt, J., Lee-Thorp, J.A., Sponheimer, M., de Ruiter, D.J. and Codron, J. (2005) Utilization of savanna-based resources by Plio-Pleistocene baboons, *South African Journal of Science*, vol.101, pp.245-248.

Colombo, A., Coqueugniot, H., Dutailly, B., Desbarats, P. and Tillier, A.-M. (2012) Nouvelles données sur l'édification des molaires et l'estimation de l'âge dentaire des enfants par imagerie médicale et 3D: apports et perspectives, *Bulletins et Mémoires de la Société d'Anthropologie de Paris*, DOI 10.1007/s13219-012-0076-4.

Conroy G.C. and Vannier, M.W. (1984) Noninvasive three dimensional computer imaging of matrix filled fossil skulls by high resolution computed tomography, *Science,* vol.226, pp.457-458.

Cook, J. (1986) The application of scanning electron microscopy to taphonomy and archaeological problems, In: Roe, D.A. (ed.) *Studies in the Upper Palaeolithic of Britain and Northwest Europe*. British Archaeological Reports International Series, vol.296, pp.143-163: Oxford.

Cooke, H.B.S. (1991) *Dinofelis barlowi* (Mammalia, Carnivore, Felidae) cranial material from Bolt's Farm, collected by the University of California African expedition, *Palaeontologia Africana*, vol.28, pp.9-21.

Copeland, S.R., Sponheimer, M., de Ruiter, D.J., Lee-Thorp, J.A., Codron, D., le Roux, P.J., Grimes, V. and Richards, M.P. (2011) Strontium isotope evidence for landscape use by early hominins, *Nature*, vol.474, pp.76-79.

Costamagno, S. (1999a) Stratégies de Chasse et Fonction des Sites au Magdalénien dans le Sud de la France, Ph.D thesis, Université Bordeaux 1, Talence.

Costamagno, S. (1999b) Coudoulous II : taphonomie d'un aven-piège. Contribution des accumulations d'origine naturelle à l'interprétation des archéofaunes du Paléolithique moyen, *Anthropozoologica*, vol.29, pp.13-31.

Costamagno, S., Robert, I., Laroulandie, V., Mourre, V. and Thiébaut, C. (2008) Rôle du gypaète barbu (*Gypaetus barbatus*) dans la constitution de l'assemblage osseux de la grotte du Noisetier (Fréchet-Aure, Hautes-Pyrénées, France), *Annales de Paléontologie*, vol.94, pp.245-265.

Coumont, M.-P. (2009) Proposition d'un référentiel taphonomique fossile de faunes issues d'avens-pièges, *Annales de Paléontologie*, vol.95, pp.1-20.

Cowlishaw, G. (1994) Vulnerability to predation in baboon populations, *Behaviour*, vol.131, pp.293-304.

Crader, D.C. (1983) Recent single-carcass bone scatters and the problem of "butchery" sites in the archaeological record, In: Clutton-Brock J. and Grigson, C. (eds.) *Animals and Archaeology. Hunters and Their Prey*, vol. 1, British Archaeological Reports International Series, vol.163, pp.107-141: Oxford.

Crowder, C. and Austin, D. (2005) Age ranges of epiphyseal fusion in the distal tibia and fibula of contemporary males and females, *Journal of Forensic Sciences*, vol.50, no.5, pp.1-7.

Cruz-Uribe K. (1991) Distinguishing hyaena from hominid bone accumulations, *Journal of Field Archaeology*, vol.18, pp.467-486.

Cukrowska, E.M., McCarthy, T.S., Pole, S., Backwell, L. and Steininger, C. (2005) The chemical removal of manganese dioxide coatings from fossil bones from the Cradle of Humankind, South Africa, *South African Journal of Sciences*, vol.101, pp.1-3.

Cumming, D.H.M. (1975) A field study of the ecology and behaviour of warthog, *Trustees of the National Museums and Monuments of Rhodesia,* vol.7, pp.1-179.

Curnoe, D. (2010) A review of early *Homo* in southern African focusing on cranial, mandibular and dental remains, with the description of a new species (*Homo gautengensis* sp.nov.), *HOMO, Journal of Comparative Human Biology*, vol.61, pp.151-177.

Curnoe, D. and Tobias, P.V (2006) Description, new reconstruction, comparative anatomy and classification of the Sterkfontein Stw 53 cranium with discussions about the taxonomy of other southern African early *Homo* remains, *Journal of Human Evolution*, vol.50, pp.36-77.

Cutler, A., Britt, B., Scheetz, R. And Cotton, J. (2011) The opisthotonic death pose as a function of muscle tone and aqueous immersion, *71st Annual Meeting of the Society of Vertebrate Paleontology*, Las Vegas, 2-5 November 2011, p.95.

Damiani, R., Modesto, S., Yates, A. and Neveling, J. (2003) Earliest evidence of cynodont burrowing, *Proceedings of the Royal Society of London*, vol.270, pp.1747-1751.

Dart, R.A. (1925) *Australopithecus africanus*: The man-ape of South Africa, *Nature*, vol.115, pp.195-199.

Dart, R.A. (1948a) The Makapansgat proto-human *Australopithecus Prometheus*, *American Journal of Physical Anthropology*, vol.6, pp.259-284.

Dart, R.A. (1948b) The adolescent mandible of *Australopithecus Prometheus*, *American Journal of Physical Anthropology*, vol.6, no.4, pp.391-412.

Dart, R.A. (1949) Innominate fragments of *Australopithecus Prometheus*, *American Journal of Physical Anthropology*, vol.7, no.3, pp.301-334.

Dart, R.A. (1953) The predatory transition from ape to man, *International Anthropological and Linguistic Review*, vol.1, pp.201-218.

Dart, R.A. (1956) Cultural status of the South African man-apes, *Smithsonian Report*, no.4240, pp.317-338.

Dart, R.A. (1957) *The Osteodontokeratic Culture of* Australopithecus Prometheus, Transvaal Museum Memoirs, no.10: Pretoria.

Dart, R.A. and Craig, D. (1959) *Adventures with the Missing Link*. Harper: New York.

Davis, S. J. M. (1987) *The Archaeology of Animals*. Yale University Press: New Haven.

de Buisonjé, P.H. (1985) Climatological conditions during deposition of the Solnhofen limestones, In: Hecht, M.K., Ostrom, J.H., Viohl, G. and Wellnhofer, P. (eds.) *The Beginnings of Birds: Proceedings of the International Archaeopteryx Conference*, 1984, pp.45-65, Freunde des Jura-Museums: Eichstätt.

Deecke, W. (1915). Paläontologische Betrachtungen. VII. Übercrustaceen, *Neues Jahrbuch für Mineralogie, Geologie, und Paläontologie*, vol.1, pp.112-126.

Defleur, A., White, T., Valensi, P., Slimak, L. and Crégut-Bonnoure, É. (1999) Neanderthal cannibalism at Moula-Guercy, Ardèche, France, *Science*, vol.286, pp.128-131.

Delson E. (1988) Chronology of South African australopith site units, In: Grine, F. (ed.) *Evolutionary History of the "Robust" Australopithecines*, pp. 317-324. Aldine de Gruyter: New York.

d'Errico, F. and Villa, P. (1997) Holes and grooves: the contribution of microscopy to the problem of art origins, *Journal of Human Evolution*, vol.33, pp.1-31.

d'Errico, F., Backwell, L. and Berger, L.R. (2001) Bone tool use in termite foraging by early hominids and its impact on our understanding of early hominid behaviour, *South African Journal of Science*, vol.97, pp.71-75.

Derry, D.E. (1911) Damage done to skills and bones by termites, *Nature*, vol.86, pp.245–246.

de Ruiter, D.J. (2001) A Methodological Analysis of the Relative Abundance of Hominids and Other Macromammals from the Site of Swartkrans, South Africa, Ph.D. thesis, University of the Witwatersrand, Johannesburg.

de Ruiter, D.J. (2003) Revised faunal lists for Members 1-3 of Swartkrans, South Africa, *Annals of the Transvaal Museum*, vol.40, pp.29-41.

de Ruiter, D.J. and Berger, L.R. (2000) Leopards as taphonomic agents in dolomitic caves - implications for bone accumulation in the hominid-bearing deposits of South Africa, *Journal of Archaeological Science*, vol.27, pp.665-684.

de Ruiter, D.J., Sponheimer, M. and Lee-Thorpe, J. (2008) Indications of habitat association of *Australopithecus robustus* in the Cradle of Humankind, South Africa, *Journal of Human Evolution*, vol.55, pp.1015-1030.

de Ruiter, D.J., Pickering, R., Steininger, C.M., Kramers, J.D., Hancox, P.J., Churchill, S.E., Berger, L.R. and Backwell, L.R. (2009) New *Australopithecus robustus* fossils and associated U-Pb dates from Cooper's Cave (Gauteng, South Africa), *Journal of Human Evolution*, vol.56, pp.497-513.

DeSilva, R., Patel, B.A. and Steininger, C. (in prep.) Cercopithecoid primate postcranial fossils from Cooper's D, South Africa.

DeVore, I. (1963) Comparative ecology and behavior of monkeys and apes, In: Washburn, S.L. (ed.) *Classification and Human Evolution*, pp. 301-319. Library of Congress: New York.

Dillon, L.C. (1997) Insect Succession on Carrion in Three Biogeographic Zones in British Columbia, M.Sc. thesis, Simon Fraser University, Burnaby.

Dirkmaat, D.C., Cabo, L.L., Ousley, S.D. and Aymes, S.A. (2008) New perspectives in forensic anthropology, *Yearbook of Physical Anthropology*, vol.51, pp.33-52.

Dirks, P.H.G.M. and Berger, L.R. (2012) Hominin-bearing caves and landscape dynamics in the Cradle of Humankind, South Africa, *Journal of African Earth Sciences*, vol.78, pp.109-131.

Dirks, P.H.G.M., Kibii, J.M., Kuhn, B.F., Steininger, C., Churchill, S.E., Kramers, J.D., Pickering, R., Farber, D.L., Mériaux, A.-S., Herries, A.I.R., King, G.C.P. and Berger, L.R. (2010) Geological setting and age of *Australopithecus sediba* from Southern Africa, *Science*, vol.328, pp.205-208.

Dodson, P. (1973) The significance of small bones in palaeoecological interpretation, *University of Wyoming Contributions to Geology*, vol.12, pp.15-19.

Dominato, V.H., Mothé, D., Avilla, L.S. and Bertoni-Machados, C. (2009) Ação de insectos em vértebras de *Stegomastodon Waringi* (Mammalia, Gomphotheriidae) do Pleistoceno de Águas de Araxá, Minas Gerais, Brasil, *Revista Brasileira de Paleontologia*, vol.12, no.1, pp.77-82.

Domínguez-Rodrigo, M. (1999) Flesh availability and bone modifications in carcasses consumed by lions: palaeoecological relevance in hominid foraging patterns, *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol.149, pp.373-388.

Domínguez-Rodrigo, M. and Piqueras, A. (2003) The use of tooth pits to identify carnivore taxa in tooth-marked archaeofaunas and their relevance to reconstruct hominid carcass processing behaviours, *Journal of Archaeological Science*, vol.30, pp.1385-1391.

Domínguez-Rodrigo, M. and Pickering, T.R. (2010) A multivariate approach for discriminating bone accumulations created by spotted hyaenas and leopards: harnessing actualistic data from East and Southern Africa, *Journal of Taphonomy*, vol.8, no.2-3, pp.155-179.

Domínguez-Rodrigo, M., Egeland, C.P. and Barba, R. (2007) The "physical attribute" taphonomic approach, In: Domínguez-Rodrigo, M., Barba, R. and Egeland, C.P. (eds.) *Deconstructing Olduvai, a Taphonomic Overview of the Bed I Sites*, pp.23-32, Springer.

Domínguez-Rodrigo, M., Juana, S. de, Galán, A.B. and Rodríguez, M. (2009) A new protocol to differentiate trampling marks from butchery marks, *Journal of Archaeological Science*, vol.36, pp.2643-2654.

Domínguez-Solera, S.D. and Domínguez-Rodrigo, M. (2009) A taphonomic study of bone modification and of tooth-mark patterns on long limb bone portions by suids, *International Journal of Osteoarchaeology*, vol.19, no.3, pp.345-363.

Domínguez-Solera, S.D. and Domínguez-Rodrigo, M. (2011) A taphonomic study of a carcass consumed by griffon vultures (*Gyps fulvus*) and its relevance for the interpretation of bone surface modifications, *Archaeological Anthropological Science*, vol.3, pp.385-392.

Douglas, R.M. (2009) A New Perspective on the Geohydrological and Surface Processes Controlling the Depositional Environment at the Florisbad Archaeozoological Site, Ph.D. thesis, University of the Free State, Bloemfontein.

Duday, H. (1990) Observations ostéologiques et décomposition du cadavre : sépulture colmatée ou en espace vide, *Revue archéologique du Centre de la France*, Tome 29, fascicule 2, pp.193-196.

Duday, H. (2009) *The Archaeology of the Dead. Lectures in Archaeothanatology*. Oxbow Books.

Duday, H., Courtaud, P., Crubézy, É., Sellier, P. and Tillier, A.-M. (1990) L'Anthropologie "de terrain": reconnaissance et interprétation des gestes funéraires, *Bulletins et Mémoires de la Société d'Anthropologie de Paris, Nouvelle Série*, Tome 2, no.3-4, pp.29-49.

Dupras, T., Schultz, J.J., Wheeler, S.M. and Williams, L.J. (2011) *Forensic Recovery of Human Remains, Archaeological Approaches*, CRC Press.

Eberth, D.A., Xing X. and Clark, J.M. (2010) Dinosaur death pits from the Jurassic of China, *Palaios*, vol.25, pp.112-125.

Efremov, I.A. (1940) Taphonomy: a new branch of paleontology, *Pan-American Geologist*, vol.74, pp.81-93.

Egeland, C.P., Domínguez -Rodrigo, M. and Barba, R. (2007) Geological and paleoecological overview of Olduvai Gorge, In: Domínguez -Rodrigo, M., Barba, R. and Egeland, C.P. (eds.) *Deconstructing Olduvai. A Taphonomic Study of the Bed I Sites*, pp.33-38, Springer.

Eickhoff, S. and Herrmann, B. (1985) Surface marks on bones from a Neolithic collective grave (Odagsen, Lower Saxony). A study on differential diagnosis, *Journal of Human Evolution*, vol.14, pp.263-274.

Eitzman, W.I. (1958) Reminiscences of Makapansgat limeworks and its bone-breccial layers, *South African Journal of Science*, vol.54, no.7, pp.177-182.

Elgin, R.A., Hone, D.W.E. and Frey, E. (2011) The extent of the pterosaur flight membrane, *Acta Palaeontologica Polonica*, vol.56, no.1, pp.99-111.

Ellison, G.T.H. (1990) The effect of scavenger mutilation on insect succession at impala carcasses in southern Africa, *Journal of Zoology*, vol.220, pp.679-688.

Eriksson, K.A. and Truswell, J.F. (1974) Stratotypes from the Malmani Subgroup northwest of Johannesburg, South Africa, *Transvaal Geological Society of South Africa*, vol.77, pp.211-222.

Esterhuysen, A.B., Sanders, V.M. and Smith, J.M. (2009) Human skeletal and mummified remains from the AD1854 siege of Mugombane, Limpopo South Africa, *Journal of Archaeological Science*, vol.36, pp.1038-1049.

Faux, C.M. and Padian, K. (2007) The opisthotonic posture of vertebrate skeletons: post-mortem contraction or death throes? *Paleobiology*, vol.33, no.2, pp.201-226.

Feibel, C.S. and Brown, F.H. (1993) Chapter 3. Microstratigraphy and paleoenvironments, In: Walker, A. and Leakey, R. (eds.) *The Nariokotome* Homo erectus *Skeleton*, Harvard University Press, Cambridge, pp.21-39.

Fejfar, O. and Kaiser, T.M. (2005) Insect bone-modification and paleoecology of Oligocene mammal-bearing sites in the Doupov Mountains, Northwestern Bohemia, *Palaeontologia Electronica*, vol.8, pp.1-11.

Fernández-López, S.R. and Fernández-Jalvo, Y. (2002) The limit between biostratinomy and fossildiagenesis, In: de Renzi, M., Alonso, M.V.P., Belinchón, M., Peñalver, E., Montoya, P. and Máarquez-Aliaga, A. (eds.) *Current Topics on Taphonomy and Fossilization*, pp.27-36

Fernández-Jalvo, Y., Díez, J.C., Cáceres, I. and Rosell, J. (1999) Human cannibalism in the Early Pleistocene of Europe (Gran Dolina, Sierra de Atapuerca, Burgos, Spain), *Journal of Human Evolution*, vol.37, pp.591-622.

Fernández-Jalvo, Y. and Andrews, P. (2003) Experimental effects of water abrasion on bone fragments*, Journal of Taphonomy*, vol.1, no.3, pp.147-163.

Fernández-Jalvo, Y. and Andrews, P. (2011) When humans chew bones, *Journal of Human Evolution*, vol.60, no.1, pp.117-123.

Fiedler, S. and Graw, M. (2003) Decomposition of buried corpses, with special reference to the formation of adipocere, *Naturwissenschaften*, vol.90, pp.291-300.

Fiorillo, A.R. (1984) An introduction to the identification of trample marks, *Current Research University of Maine*, vol.1, pp.47-48.

Fischer, J.W. (1995) Bone surface modifications in zooarchaeology, *Journal of Archaeological Method and Theory*, vol.2, no.1, pp.7-68.

Fowler, W.R. (1984) Late Preclassic mortuary patterns and evidence for human sacrifice at Chalchuapa, El Salvador, *American Antiquity*, vol.49, no.3, pp.603-618.

Fordyce, N., Smith, R. and Chinsamy, A. (2012) Evidence of a therapsid scavenger in the Late Permian Karoo Basin, South Africa, *South African Journal of Science*, vol.108, no.11/12, pp.1-4.

Freedman, L. (1957) The fossil Cercopithecoidea of South Africa, *Annals of the Transvaal Museum*, vol.23, no.2, pp.121-262.

Freedman, L. (1976) South African fossil Cercopithecoidea: a re-assessment including a description of new material from Makapansgat, Sterkfontein and Taung, *Journal of Human Evolution*, vol.5, pp.297-315.

Frey, E. and Martill, D.M. (1994) A new pterosaur from the Crato Formation (Lower Cretaceous, Aptian) of Brazil, *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, vol.194, pp.379-412.

Fosse, P. (1994) Taphonomie Paléolithique : les Grands Mammifères de Soleihac (Haute-Loire) et de Lunel-Viel (Hérault), Ph.D. thesis, Université de Provence-Aix-Marseille.

Galdikas, B.M.F. (1978) Orangutan death and scavenging by pigs, *Science*, vol.200, pp.68-70.

Gargett, R.H. (1989a) Grave shortcomings, the evidence for Neandertal burial, *Current Anthropology*, vol.30, no.2, pp.157-190.

Gargett, R.H. (1989b) On the evidence for Neandertal burial, *Current Anthropology*, vol.30, no.3, pp.322-330.

Gargett, R.H. (1999) Middle Palaeolithic burial is not a dead issue: the view from Qafzeh, Saint-Césaire, Kebara, Amud, and Dederiyeh, *Journal of Human Evolution*, vol.37, pp.27-90.

Gennard, D. (2012) *Forensic entomology, An Introduction.* Wiley-Blackwell Publishers, Second edition.

Georgi, J.A. and Krause, D.W. (2010) Postcranial axial skeleton of *Simosuchus clarki* (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagascar, *Journal of Vertebrate Paleontology*, vol.30, supplement to no.6, pp.99-121.

Gifford, D.P. and Crader, D.C. (1977) A computer coding system for archaeological faunal remains, *American Antiquity*, vol.42, pp.225-238.

Gilbert, C.C. (2008) African Papionin Phylogenetic History and Plio-Pleistocene Biogeography, Ph.D thesis, Stony Brook University, Stony Brook, New-York.

Gillette, D.D. (1994) Seismosaurus: *the Earth Shaker*. Columbia University Press: New York.

Gommery, D., Sénégas, F., Thackeray, J.F., Potze, S.,Kgasi, L., Claude, J. and Lacruz, R. (2008) Plio-Pleistocene fossils from Femur Dump, Bolt's Farm, Cradle of Humankind World Heritage Site, *Annals of the Transvaal Museum*, vol.45, pp.67-76.

Gommery, D., Badenhorst, S., Sénégas, F., Potze, S. and Kgasi, L. (2012) Minnaar's Cave: a Plio-Pleistocene site in the Cradle of Humankind, South Africa: its history, location, and fauna, *Annals of the Ditsong National Museum of Natural History*, vol.2, pp.19-31.

Goodall, J. (1986) *The Chimpanzees of Gombe: Patterns of Behavior*. Cambridge: Harvard University.

Goodall, J., Bandora, A., Bergmann, E., Busse, C., Matama, H. and Russ, D. (1979) Intercommunity interactions in the population of chimpanzees in the Gombe National Park, In: Hamburg, D.A. and McKown, E.R. (eds.) *The Great Apes*, pp.13-54. Benjamin Cummings: Menlo Park.

Gow, C.E. (1973) Habitual sheltering in an extensive cave system by baboons near Bredasdorp, South Africa. *South African Journal of Science*, vol.69, p.182.

Gradziński, R. (1969) Sedimentation of dinosaur-bearing Upper Cretaceous deposits of the Nemegt Basin, Gobi Desert, *Palaeontologica Polonica*, no.21, pp.147-229.

Greenfield, H.J. (1988) Bone consumption by pigs in a contemporary Serbian village: implications for the interpretation of prehistoric faunal assemblages, *Journal of Field Archaeology*, vol.15, pp.473-479.

Grigson, C. (1982) Porridge and pannage: pig husbandry in Neolithic England, In: Limbrey, S. and Bell, M. (eds.) *Archaeological Aspects of Woodland Ecology,* British Archaeological Reports International Series, vol.146, pp.297-314: Oxford.

Grine, F.E. (1989) New hominid fossils from the Swartkrans Formation (1979-1986 excavations): craniodental specimens, *American Journal of Physical Anthropology*, vol.79, pp.409-449.

Grine, F.E. (1993) Description and preliminary analysis of new hominid craniodental fossils from the Swartkrans Formation, In: Brain, C.K. (ed.) *Swartkrans: A Cave's Chronicle of Early Man*, pp.75-116. Transvaal Museum Monograph No.8: Pretoria.

Grine, F.E. (2005) Early *Homo* at Swartkrans, South Africa: a review of the evidence and an evaluation of recently proposed morphs, *South African Journal of Science*, vol.101, pp.43-52.

Grobler, J. and Wilson, V. (1972) Food of the leopard *Panthera pardus* (Linn.) in the Rhodes Matopos National Park, Rhodesia, as determined by faecal analysis, *Arnoldia*, vol.5, pp.1-9.

Guyomarc'h, P., Santos, F., Dutailly, B., Desbarats, P., Bou, C. and Coqueugniot, H. (2012) Three-dimensional computer-assisted craniometrics: a comparison of the uncertainty in measurement induced by surface reconstruction performed by two computer programs, *Forensic Science International*, vol.219, no.1-3, pp.221-227.

Haefner, J.N., Wallace, J.R. and Merritt, R.W. (2004) Pig decomposition in lotic aquatic systems: the potential use of algal growth in establishing a post-mortem submersion interval (PMSI), *Journal of Forensic Sciences*, vol.49, no.2, pp.1-7.

Haglund, W.D. (1992) Contribution of rodents to post-mortem artifacts of bone and soft tissue, *Journal of Forensic Sciences*, vol.37, no.6, pp.1459-1465.

Haglund, W.D. and Sorg, M.H. eds (2002) *Advances in Forensic Taphonomy: Method, Theory, and Archaeological Perspectives*, Boca Raton: CRC Press.

Haglund, W.D., Reay, D.T. and Swindler, D.R. (1989) Canid scavenging/disarticulation sequence of human remains in the Pacific Northwest, *Journal of Forensic Sciences*, vol.34, no.3, pp.587-606.

Hamilton, W. (1982) Baboon sleeping site preferences and relationships to primate grouping patterns, *American Journal of Primatology*, vol.3, pp.41-53.

Handler, J.S. (1996) A prone burial from a plantation slave cemetery in Barbados, West Indies: possible evidence for an African-type witch or other negatively viewed person, *Historical archaeology*, vol.30, no.3, pp.76-86.

Hanson, C.B. (1980) Fluvial taphonomic processes: models and experiments, In: Behrensmeyer, A.K. and Hill, A. (eds.) *Fossils in the Making*, pp.156-181. University Chicago Press: Chicago.

Harrold, F.B. (1980) A comparative analysis of Eurasian Palaeolithic burials, *World Archaeology*, vol.12, no.2, pp.195-211.

Hart, D. (2000) Primates as prey: ecological, morphological and behavioral relationships between primate species and their predators, Ph.D. thesis, Washington University, St-Louis.

Hartstone-Rose, A., de Ruiter, D.J., Berger, L.R. and Churchill, S.E. (2007) A sabre-tooth felid from Coopers Cave (Gauteng, South Africa) and its implications for *Megantereon* (Felidae: Machairodontinae) taxonomy, *Palaeontologia africana*, vol.42, pp.99-108.

Hartstone-Rose, A., Kuhn, B.F., Nalla, S., Werdelin, L. and Berger, L.R. (2013) A new species of fox from the *Australopithecus sediba* type locality, Malapa, South Africa, *Transactions of the Royal Society of South Africa*, DOI:10.1080/0035919X.2012.748698, pp.1-9.

Hasiotis, S.T. (2004) Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain Region, USA: paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses, *Sedimentary Geology*, vol.167, pp.177-268.

Hasiotis, S.T., Fiorillo, A.R. and Hanna, R.R. (1999) Preliminary report on borings in Jurassic dinosaur bones: evidence for invertebrate-vertebrate interactions, In: Gillette, D.D. (ed.) *Miscellaneous Publication Utah Geological Survey*, pp.193-200.

Haynes, G. (1980) Evidence of carnivore gnawing on Pleistocene and recent mammalian bones, *Paleobiology*, vol.6, no.3, pp.341-351.

Haynes, G. (1983a) A guide for differentiating mammalian carnivore taxa responsible for gnaw damage to herbivore limb bones, *Paleobiology*, vol.9, no.2, pp.164-172.

Haynes, G. (1983b) Frequencies of spiral and green-bone fractures on ungulate limb bones in modern surface assemblages, *American Antiquity*, vol.48, pp.102-114.

Haynes, G. and Stanford, D. (1984) On the possible utilization of *Camelops* by early Man in North America, *Quaternary Research*, vol.22, pp.216-230.

Heinroth, O. (1923) Die Flügel von *Archaeopteryx*, *Journal of Ornithology*, vol.71, pp.277-283.

Henry, A.H., Ungar, P.S., Passey, B.H., Sponheimer, M., Rossouw, L., Bamford, M., Sandberg, P., de Ruiter, D.J. and Berger, L.R. (2012) The diet of *Australopithecus sediba*, *Nature*, vol.487, pp.90-93.

Herrero Cortés, J. (2001) Adaptación Functional del Jabalí (*Sus scrofa* L.) a un Ecosistema Forestall y a un Sistema Agrario Intensive en Aragón, Ph.D. thesis, University of Madrid.

Herries, A.I.R. (2003) Magnetostratigraphic Seriation of South African Hominin Palaeocaves, Ph.D. thesis, University of Liverpool.

Herries, A.I.R., Curnoe, D. and Adams, J.W. (2009) A multi-disciplinary seriation of early *Homo* and *Paranthropus* bearing palaeocaves in southern Africa, *Quaternary international*, vol.202, pp.14-28.

Herries, A.I.R. and Shaw, J. (2011) Palaeomagnetic analysis of the Sterkfontein palaeocave deposits: Implications for the age of the hominin fossils and stone tool industries, *Journal of Human Evolution*, vol.60, pp.523-539.

Hill, A. (1979a) Disarticulation and scattering of mammal skeletons, *Paleobiology*, vol.5, no.3, pp.261-274.

Hill, A. (1979b) Butchery and natural disarticulation: an investigatory technique, *American Antiquity*, vol.44, no.4, pp.739-744.

Hill, A. (1987) Damage to some fossil bones from Laetoli, In: Leakey, M.D. and Harris, J.M. (eds.) *Laetoli: A Pliocene Site in Northern Tanzania*, pp.543-545. Clarendon Press: Oxford.

Hill, A. (1989) Bone modification by modern spotted hyaenas, In: Bonnichsen R. and Sorg, M.H. (eds.) *Bone Modification, Center for the Study of the First Americans*, pp.169-178. Orono, ME.

Hill, A. and Walker, A. (1972) Procedures in vertebrate taphonomy; notes on a Ugandan Miocene fossil locality, *Journal of the Geological Society of London*, vol.128, pp.399-406.

Hill, A. and Behrensmeyer, A.K. (1984) Disarticulation patterns of some modern East African mammals, *Paleobiology*, vol.10, no.3, pp.366-376.

Hilton-Barber, B. and Berger, L.R. (2002) *Field Guide to the Cradle of Humankind. Sterkfontein, Swartkrans, Kromdraai and Environs World Heritage Site,* Struik Publishers.

Howie, F.M.P. (1974) Introduction of thioglycollic acid in preparation of vertebrate fossils, *Curator: The Museum Journal*, vol.17, no.2, pp.159-166.

Huchet J.-B., Deverly, D., Gutierrez, B. and Chauchat, C. (2011) Taphonomic evidence of a human skeleton gnawed by termites in a Moche-Civilisation Grave at Huaca de la Luna, Peru, *International Journal of Osteoarchaeology*, vol.21, pp.92-102.

Hughes, A.R. (1954) Hyaenas versus Australopithecines as agents of bone accumulation, *American Journal of Physical Anthropology*, vol.12, no.4, pp.467-486.

Hughes, A.R. and Tobias, P.V. (1977) A fossil skull probably of the genus *Homo* from Sterkfontein, Transvaal, *Nature*, vol.265, pp.310-312.

Introna, F., De Donno, A., Santoro, V., Corrado, S., Romano, V., Porcelli, F. and Campobasso, C.P. (2011) The bodies of two missing children in an enclosed underground environment, *Forensic Science International*, vol.207, no.1-3, pp.40-47.

Iwamoto, T. and Dunbar, R.I.M. (1983) Thermoregulation, habitat quality and the behavioural ecology of gelada baboons, *Journal of Animal Ecology*, vol.52, no.2, pp.357-366.

Janaway, R.C. (1987) The preservation of organic materials in association with metal artefacts deposited in inhumation graves, In: Boddington, A., Garland, A.N. and Janaway, R.C. (eds.) *Death, Decay and Reconstruction: Approaches to Archaeology and Forensic Science*, pp.127-141. Manchester University Press: Manchester.

Jay, P. (1965) Field studies, In: Schrier, A.M., Harlow, H.F. and Stollnitz, F. (eds.) *Behaviour of Non human primates*, pp.525-591. Academic Press: New York.

Jennings, D.S. and Hasiotis, S.T. (2006) Taphonomic analysis of a dinosaur feeding site using geographic information systems (GIS), Morrison Formation, Southern Bighorn Basin, Wyoming, USA, *PALAIOS*, vol.21, pp.480-492.

Jewell, P.A. (1966) The concept of home range in mammals, *Symposia of the Zoological Society of London*, vol.18, pp.85-109.

Jit, I., Sehgal, S. and Sahni, D. (2001) An Indian mummy: a case report, *Forensic Science International*, vol.117, pp.57-63.

Johanson, D.C. and Taieb, M. (1976) Plio-Pleistocene hominid discoveries in Hadar, Ethiopia, *Nature*, vol.260, pp.293-297.

Johanson, D.C., White, T. and Coppens, Y. (1978) A new species of the genus *Australopithecus* (Primates: Hominidae) from the Pliocene of eastern Africa, *Kirtlandia*, no.28, pp.1-14.

Johanson, D.C. and White, T.D. (1979) A systematic assessment of early African hominids, *Science*, vol.203, pp.321-330.

Johanson, D. C. and Edey, M.A. (1982) *Lucy. The Beginnings of Humankind*. Warner Books Editions.

Johanson, D.C., Taieb, M. and Coppens, Y. (1982) Pliocene Hominids from the Hadar Formation, Ethiopia (1973-1977): stratigraphic, chronologic, and paleoenvironmental contexts, with notes on hominid morphology and systematic, *American Journal of Physical Anthropology*, vol.57, pp.373-402.

Johnson, E. (1985) Current developments in bone technology, In: M. B. Schilfer (ed.) *Advances in Archaeological Method and Theory,* vol.8, pp. 157-235. Orlando: Academic Press.

Jones, M.A. (1984) Seasonal changes in the diet of bushpig, *Potamochoerus porcus* Linn., in the Matopos National Park, *South African Journal of Wild Life Research*, vol.14, pp.97-100.

Jones, B. (2001) Microbial activity in caves – a geological perspective, *Geomicrobiology Journal*, vol.18, pp.345-357.

Kaiser, T.M. (2000) Proposed fossil insect modification to fossil mammalian bone from Plio-Pleistocene hominid-bearing deposits of Laetoli (Northern Tanzania), *Annals of the Entomological Society of America*, vol.93, pp.693-700.

Kaiser, T.M. and Katterwe, H. (2001) The application of 3D-microprofilometry as a tool in the surface diagnosis of fossil and sub-fossil vertebrate hard tissue. An example from the

Pliocene Upper Laetolil Beds, Tanzania, *International Journal of Osteoarchaeology*, vol.11, pp.350-356.

Kawabe, M. (1966) One observed case of hunting behavior among wild chimpanzees living in the savanna woodland of western Tanzania, *Primates*, vol.7, no.3, pp.393-396.

Kelly, J.A., van der Linde, T.C. and Anderson, G.S. (2009) The influence of clothing and wrapping on carcass decomposition and arthropod succession during the warmer seasons in Central South Africa, *Journal of Forensic Sciences*,vol.54, no.5, pp.1-8.

Keyser, A.W. (1991) The palaeontology of Haasgat. A preliminary account, *Palaeontologia Africana*, vol.28, pp.29-33.

Keyser, A.W. (2000) The Drimolen skull: the most complete australopithecine cranium and mandible to date, *South African Journal of Science*, vol.96, pp.189-193.

Keyser, A.W. and Martini, J.E.J. (1991) Haasgat: a new Plio-Pleistocene fossil occurrence, *Palaeoecology of Africa*, vol.21, pp.19-129.

Keyser, A.W., Menter, C.G., Moggi-Cecchi, J., Pickering, T.R. and Berger, L.R. (2000) Drimolen: a new hominid-bearing site in Gauteng, South Africa, *South African Journal of Science*, vol.96, pp.193-197.

Kibii, J.M. (2004) Comparative Taxonomic, Taphonomic and Palaeoenvironmental Analysis of 4-2.3 million Year Old Australopithecine Cave Infills at Sterkfontein, Ph.D. thesis, University of the Witwatersrand, Johannesburg.

Kibii, J.M. (2007) Taxonomy, taphonomy and palaeoenvironment of hominid and non-hominid primates from the Jacovec Cavern, Sterkfontein, *South African Archaeological Society*, vol.62, no.186, pp.90-97.

Kibii, J. M. (2009) Taphonomic aspects of African porcupines (*Hystrix cristata*) in the Kenyan Highlands, *Journal of Taphonomy*, vol.7, no.1, pp.21-27.

Kibii, J.M., Churchill, S.E., Schmid, P., Carlson, K.J., Reed, N.D., de Ruiter, D.J. and Berger, L.R. (2011) A partial pelvis of *Australopithecus sediba*, *Science*, vol.333, pp.1407-1411.

Kim, M.J., Oh, C.S., Lee, I.S., Lee, B.H., Choi, J.H., Lim, D.-S., Yi, Y.S., Han, W.-J., Kim, Y.-S., Bok, G.D., Lee, S.D. and Shin, D.H. (2008) Human mummified brain from a medieval tomb with lime-soil mixture barrier of the Joseon dynasty, Korea, *International Journal of Osteoarchaeology*, vol.18, pp.614-623.

Kimbel, W.H., Lavi, R., Rak, Y. and Hovers, E. (1995) Hominid remains from Amud Cave in the context of the Levantine Middle Paleolithic, Paléorient, vol.21, no.2, pp.47-61.

Kitching, J. W. (1980) On some fossil arthropoda from the Limeworks, Makapansgat, Potgietersrus, *Palaeontologia Africana*, vol.23, pp.63-68.

Kjorlien, Y.P., Beattie, O.B. and Peterson, A.E. (2009) Scavenging activities can produce predictable patterns in surface skeletal remains scattering: observations and comments from two experiments, *Forensic Science International*, vol.188, pp.103-106.

Klein, R.G. and Cruz-Uribe, K. (1984) *The Analysis of Animal Bones from Archaeological Sites*, University of Chicago Press: Chicago.

Klippel, W.E. and Synstelien, J.A. (2007) Rodents as taphonomic agents: bone gnawing by brown rats and gray squirrels, *Journal of Forensic Sciences*, vol.52, no.4, pp.765-773.

Klein, R.G., Cruz-Uribe, K. and Beaumont, P.B. (1991) Environmental, ecological, and paleoanthropological implications of the Late Pleistocene mammalian fauna from Equus Cave, Northern Cape Province, *Quaternary Research,* vol.36, pp.94-119.

Knüsel, C.J., Janaway, R.C. and King, S.E. (1996) Death, decay, and ritual reconstruction: archaeological evidence of cadaveric spasm, *Oxford Journal of Archaeology*, vol.15, no.2, pp.121-128.

Kos, A.M. (2003a) Pre-burial taphonomic characterization of a vertebrate assemblage from a pitfall cave fossil deposit in southeastern Australia, *Journal of Archaeological Science*, vol.30, pp.769-779.

Kos, A.M. (2003b) Characterization of post-depositional taphonomic processes in the accumulation of mammals in a pitfall cave deposit from southeastern Australia, *Journal of Archaeological Science*, vol.30, pp.781-796.

Kreutzer, L.A. (1992) Bison and Deer bone mineral densities: comparisons and implications for the interpretation of archaeological faunas, *Journal of Archaeological Science*, vol.19, pp.271-294.

Kruuk, H. (1972) *The Spotted Hyaena: A Study of Predation and Social Behaviour*. Chicago: University of Chicago Press.

Kulshrestha, P. and Satpathy, D.K. (2001) Use of beetles in forensic entomology, *Forensic Science International*, vol.120, pp.15-17.

Kuhn, B.F. (2006) The Collection Behaviour and Taphonomic Signatures of Hyaenids, Ph.D. thesis, University of Pretoria.

Kuhn, B.F., Berger, L.R. and Skinner, J.D. (2010) Examining criteria for identifying and differentiating fossil faunal assemblages by hyenas and hominins using extant hyenid accumulations, *International Journal of Osteoarchaeology*, vol.20, pp.15-35.

Kuhn, B.F., Werdelin, L., Hartstone-Rose, A., Lacruz, R.S. and Berger, L.R. (2011) Carnivoran remains from the Malapa hominin site, South Africa, *Plos One*, vol.6, no.11, pp.1-11.

Kuman, K. and Clarke, R.J. (2000) Stratigraphy, artefact industries and hominid associations for Sterkfontein, Member 5, *Journal of Human Evolution*, vol.38, pp.827-847.

Lacruz, R.S. (2002) Analysis of Stratified Fossil Deposits from the Gladysvale Cave, South Africa, M.Sc. thesis, University of the Witwatersrand, Johannesburg.

Lacruz, R.S. and Maude, G. (2005) Bone accumulations at brown hyena (*Parahyaena brunnea*) den sites in the Makgadikgadi Pans, Northern Botswana: taphonomic, behavioral and palaeoecological implications, *Journal of Taphonomy*, vol.3, no.1, pp.43-54.

Lacruz, R.S., Brink, J.S., Hancox P.J., Skinner, A.R., Herries, A.I.R., Schmid, P., and Berger, L.R. (2002) Palaeontology and geological context of a middle Pleistocene faunal assemblage from the Gladysvale cave, South Africa, *Palaeontologia Africana*, vol.38, pp.99-114.

Lacruz, R., Turner, A. and Berger, L.R. (2006) New *Dinofelis* (Carnivora: Machairodontinae) remains from Sterkfontein Valley sites and a taxonomic revision of the genus in southern Africa, *Annals of the Transvaal Museum*, vol.43, pp.89-106.

Lam, Y.M. (1992) Variability in the behaviour of spotted hyaenas as taphonomic agents, *Journal of Archaeological Science*, vol.19, pp.389-406.

Lam, Y.M., Chen, X., Marean, C. and Frey, C.J. (1998) Bone density and long bone representation in archaeological faunas: comparing results from CT and Photon Densitometry, *Journal of Archaeological Science*, vol.25, pp.559-570.

Lam, Y.M., Chen, X. and Pearson, O.M. (1999) Intertaxonomic variability in patterns of bone density and the differential representation of bovid, cervid, and equid elements in the archaeological record, *American Antiquity*, vol.64. no.2, pp.343-362.

Landt, M.J. (2004) Investigations of Human Gnawing on Small Mammal Bones: Among Contemporary Bofi Foragers of the Central African Republic, Ph.D. thesis, Washington State University.

Landt, M.J. (2007) Tooth marks and human consumption: ethnoarchaeological mastication research among foragers of the Central African Republic, *Journal of Archaeological Science*, vol.3, pp.1629-1640.

Langley, M.C., Clarkson, C. and Ulm, S. (2008) Behavioural complexity in Eurasian Neanderthal populations: a chronological examination of the archaeological evidence, *Cambridge Archaeological Journal*, vol.18, no.3, pp.289-307.

Latham, A.G. and Herries, A.I.R. (2004) The formation and sedimentary infilling of the Cave of Hearths and Historic Cave Complex, Makapansgat, South Africa, *Geoarchaeology: An International Journal*, vol.19, no.4, pp.323-342.

Latham, A.G., Herries, A.I.R., Quinney, P., Sinclair, A. and Kuykendall, K. (1999) The Makapansgat Australopithecine site from a speleological perspective, *Geological Society, London, Special Publications*, vol.165, pp.61-77.

Laws, R.R. (1996) Paleopathological Analysis of a Sub-Adult *Allosaurus fragilis* (MOR 693) from the Upper Jurassic Morrison Formation with Multiple Injuries and Infections, M.Sc. thesis, Montana State University, Bozeman.

Leakey, L.S.B., Tobias, P.V. and Napier, J.R. (1964) A new species of the genus *Homo* from Olduvai Gorge, *Nature*, vol.202, pp.7-9.

Leakey, M., Spoor, F., Brown, F.H., Gathogo, P.N., Kiarie, C., Leakey, L.N. and McDougall, I. (2001) New hominin genus from eastern Africa shows diverse middle Pliocene lineages, *Nature*, vol.410, pp.433-440.

Leclerc, M. (1978) Entomologie et médecine légale - datation de la mort. *Collection de médecine légale et de toxicologie médicale*, vol.108: Masson éditions.

Lee-Thorp, J.A., van der Merwe, N.J. and Brain, C.K. (1989) Isotopic evidence for dietary differences between two extinct baboon species from Swartkrans, *Journal of Human Evolution*, vol.18, pp.183-190.

Lee-Thorp, J.A., van der Merwe, N.J. and Brain, C.K. (1994) Diet of *Australopithecus robustus* at Swartkrans from stable carbon isotopic analysis, *Journal of Human Evolution*, vol.27, pp.361-372.

Le Fur, S., Fara, E., Mackaye, H.T., Vignaud, P. and Brunet, M. (2009) The mammal assemblage of the hominid site TM266 (Late Miocene, Chad Basin): ecological structure and paleoenvironmental implications, *Naturwissenschaften*, vol.96, pp.565-574.

Lingham-Soliar, T. (2011) The evolution of the feather: *Sinosauropteryx*, a colourful tail, *Journal of Ornithology*, vol.152, pp.567-577.

Lordkipanidze, D., Vekua, A., Ferring, R., Rightmire, G.P., Zollikofer, C.P.E., Ponce de León, M.S., Agusti, J., Kila, G., Mouskhelishvili, A., Nioradze, M. and Tappen, M. (2006) A fourth hominin skull from Dmanisi, Georgia, *The Anatomical Record,* Part A 288A, pp.1146-1157.

Louchart, A., Wesselman, H., Blumenschine, R.J., Hlusko, L.J., Njau, J.K., Black, M.T., Asnake, M. and White, T.D. (2009) Taphonomic, avian, and small-vertebrate indicators of *Ardipithecus ramidus* habitat, *Science*, vol.326, pp.66e1-66e4.

Luo, Z. and Ketten, D.R. (1991) CT scanning and computerized reconstructions of the inner ear of multituberculate mammals, *Journal of Vertebrate Paleontology*, vol.11, no.2, pp.220-228.

Luongo, G., Perrotta, A., Scarpati, C., De Carolis, E., Patricelli, G. and Ciarallo, A. (2003) Impact of the AD 79 explosive eruption on Pompeii, II. Causes of death of the inhabitants

inferred by stratigraphic analysis and areal distribution of the human casualties, *Journal of Volcanology and Geothermal Research*, vol.126, pp.169-200.

Lupo, K.D. (1994) Butchering marks and carcass acquisition strategies: distinguishing hunting from scavenging in archaeological contexts, *Journal of Archaeological Science*, vol.21, pp.827-837.

Lyman, R.L. (1984) Bone density and differential survivorship of fossil classes, *Journal of Anthropological Archaeology*, vol.3, pp.259-299.

Lyman, R.L. (1987a) Archaeofaunas and butchery studies: a taphonomic perspective, In: Schiffer, M.B. (ed.) *Advances in Archaeological Method and Theory*, vol.10, pp.249-337.

Lyman, R.L. (1987b) On the analysis of vertebrate mortality profiles: sample size, mortality type, and hunting pressure, *American Antiquity*, vol.52, no.1, pp.125-142.

Lyman, R.L. (1994a) Quantitative units and terminology in zooarchaeology, *American Antiquity*, vol.59, no.1, pp.36-71.

Lyman, R.L. (1994b) *Vertebrate Taphonomy*. Cambridge University Press.

Lyman, R.L. (1994c) Relative abundances of skeletal specimens and taphonomic analysis of vertebrate remains, *PALAIOS*, vol.9, p.288-298.

Lyman, R.L. and Fox, G.L. (1989) A critical evaluation of bone weathering as an indication of bone assemblage formation, *Journal of Archaeological Science*, vol.16, pp.293-317.

MacGregor, D.M. (1999a) Decomposition of pig carrion in southeast Queenland, Australia, during summer, Paper presented at 51st American Academy of Forensic Sciences Annual Meeting, Orlando, FL.

MacGregor, D.M. (1999b) Decomposition of pig carrion in southeast Queenland, Australia, during winter, Paper presented at 51st American Academy of Forensic Sciences Annual Meeting, Orlando, FL.

Maclean, G.L. (1985) *Roberts' Birds of Southern Africa*. John Voelcker Bird Book Fund.

Maguire, J.M., Pemberton, D. and Collett, M.H. (1980) The Makapansgat limeworks grey breccias: hominids, hyaenas, hystricids or hillwash?, *Palaeontologia Africana*, vol.23, pp.75-98.

Maisey, J.G. (2001) CT-scan reveals new cranial features in Devonian Chondrichthyan "*Cladodus*" *Wildungensis, Journal of Vertebrate Paleontology*, vol.21, no.4, pp.807-810.

Mallye, J.-B. (2007) Les Restes de Blaireau en Contexte Archéologique: Taphonomie, Archéozoologie et Éléments de Discussion des Séquences Préhistoriques, Ph.D. thesis, Université Bordeaux 1, Talence.

Mallye, J.-B. (2011) Badger (*Meles meles*) remains within caves as an analytical tool to test the integrity of stratified sites: The contribution of Unikoté cave (Pyrénées-Atlantiques, France), *Journal of Taphonomy*, vol.9, no.1, 15-36.

Mallye, J.-B. and Laroulandie, V. (2004) L'exploitation des petits animaux et les pièges de l'os: exemples chez les oiseaux et les mustélidés, In: Brugal, J.-P. and Desse, J. (eds.) *XXIVe rencontres internationales d'archéologie et d'histoire d'Antibes*, pp. 185-190. Éditions APDCA, Antibes.

Mann, R.W., Bass, W.M. and Meadows, L. (1990) Time since death and decomposition of the human body: variables and observations in case and experimental field studies, *Journal of Forensic Sciences*, vol.35, no.1, pp.103-111.

Manson, J.H. and Wrangham, R.W. (1991) Intergroup aggression in chimpanzees and humans, *Current Anthropology*, vol.32, no.4, pp.369-390.

Manzi, G., Bruner, E., Caprasecca, S., Gualdi, G. and Passarello, P. (2001) CT-scanning and virtual reproduction of the Saccopastore Neandertal crania, *Rivista di Antropologia (Roma)*, vol.79, pp.61-72.

Marchenko, M.I. (2001) Medicolegal relevance of cadaver entomofauna for the determination of the time of death, *Forensic Science International*, vol.120, pp.89-109.

Marean, C.W. and Spencer, L.M. (1991) Impact of carnivore ravaging on zooarchaeological measures of element abundance, *American Antiquity*, vol.56, no.4, pp.645-658.

Marean, C.W., Spencer, L.M., Blumenschine, R.J. and Capaldo, S.D. (1992) Captive hyaena bone choice and destruction, the schlepp effect and Olduvai archaeofaunas, *Journal of Archaeological Science*, vol.19, pp.101-121.

Marean, C.W. and Bertino, L. (1994) Intrasite spatial analysis of bone: subtracting the effect of secondary carnivore consumers, *American Antiquity*, vol.59, no.4, pp.748-768.

Marean, C.W. and Ehrhardt, C.L. (1995) Paleoanthropological and paleoecological implications of the taphonomy of a sabertooth's den, *Journal of Human Evolution*, vol.29, no.6, pp.515-547.

Marín Arroyo, A., Fosse, P. and Vigne, J.-D. (2009) Probable evidences of bone accumulation by Pleistocene bearded vulture at the archaeological site of El Mirón Cave (Spain), *Journal of Archaeological Science*, vol.36, pp.284-296.

Marshall, L.G. (1989) Bone modification and the "laws of burial", In: Bonnichsen, R. and Sorg, M.H. (eds.) *Bone Modification*, pp.7-24. University of Maine Center for the Study of the First Americans, Thompson-Shore Inc: USA.

Martin, D.McB., Clendenin, C.W., Krapez, B. and McNaughton, N.J. (1998) Tectonic and geochronological constraints on late Archaean and Palaeoproterozoic stratigraphic

correlation within and between the Kaapvaal and Pilbara Cratons, *Journal of the Geological Society*: London, vol.155, pp.311-322.

Martin, L.D. and West, D.L. (1995) The recognition and use of dermestid (Insecta, Coleoptera) pupation chambers in paleoecology, *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol.113, pp.303-310.

Martínez, G. (2009) Human chewing bone surface modification and processing of small and medium prey amongst the Nunak (foragers of the Colombian Amazon), *Journal of Taphonomy*, vol.7, no.1, pp.1-20.

Mason, W.A. (1968) Use of space by Callicebus groups, In: Jay, P. (ed.) *Primates*, pp. 200-216. Holt, Rinehard, Winston: New York.

Mastrolorenzo, G., Petrone, P.P., Pagano, M., Incoronato, A., Baxter, P.J., Canzanella, A. and Fattore, L. (2001) Herculaneum victims of Vesuvius in AD 79, *Nature*, vol.410, pp.769-770.

Mastrolorenzo, G., Petrone, P., Pappalardo, L. and Guarino, F.M. (2010) Lethal thermal impact at periphery of pyroclastic surges: evidences at Pompeii, *Plos One*, vol.5, no.6, pp.1-12.

Maureille, B. and Sellier, P. (1996) Dislocation en ordre paradoxal, momification et décomposition : observations et hypothèses, *Bulletins et Mémoires de la Société d'Anthropologie de Paris*, Nouvelle Série, tome 8, fascicule 3-4, pp.313-327.

McGraw, W.S., Cooke, C. and Shultz, S. (2006) Primate remains from African crowned eagle (*Stephanoaetus coronatus*) nests in Ivory Coast's Tai forest: implications for primate predation and early hominid taphonomy in South Africa, *American Journal of Physical Anthropology*, vol.131, pp.151-165.

McGrew, W., McKee, J. and Tutin, C. (2003) Primates in caves: two new reports of *Papio* spp., *Journal of Human Evolution*, vol.44, pp.521-526.

McHenry, H. (1991) Femoral lengths and stature in Plio-Pleistocene hominids, *American Journal of Physical Anthropology*, vol.85, pp.149-158.

McKee J.K. (1993) Faunal dating of the Taung hominid fossil deposit, *Journal of Human Evolution*, vol.25, pp.363-376.

McKee J.K. (1995) Further chronological seriations of southern African Pliocene and Pleistocene mammalian faunal assemblages, *Palaeontologia Africana*, vol.32, pp.11-16.

McKee, J.K. and Keyser, A.W. (1994) Craniodental remains of *Papio angusticeps* from the Haasgat cave site, South Africa, *International Journal of Primatology*, vol.15, no.6, pp.823-841.

McKee, J.K. and Tobias, P.V. (1994) Taung stratigraphy and taphonomy: preliminary results based on the 1988-1993 excavations, *South African Journal of Science*, vol.90, pp.233-235.

McKee J.K., Thackeray J.F. and Berger L.R. (1995) Faunal assemblage seriation of southern African Pliocene and Pleistocene fossil deposits, *American Journal of Physical Anthropology*, vol.96, pp.235-250.

Menter, C.G., Kuykendall, K.L., Keyser, A.W. and Conroy, G.C. (1999) First record of hominid teeth from the Plio-Pleistocene site of Gondolin, South Africa, *Journal of Human Evolution*, vol.37, pp.299-307.

Miller, G.J. (1975) A study of cuts, grooves, and other marks on recent and fossil bones: II, weathering cracks, fractures, splinters, and other similar natural phenomena, In: Swanson, E. (ed.) *Lithic Technology*, pp.212-226. The Hague: Mouton.

Mills, M.G.L. and Mills, M.E.J. (1977) An analysis of bones collected at hyaena breeding dens in the Gemsbok National parks, *Annals of the Transvaal Museum*, vol.30, no.14, pp.145-155.

Milstein, P. le S. (1971) The bushpig *Potamochoaerus porcus* as a problem animal in South Africa, *Report, Entomological Symposium Pretoria*, Mimeograph.

Mitani, J.C. and Watts, D.P. (1999) Demographic influences on the hunting behavior of chimpanzees, *American Journal of Physical Anthropology*, vol.109, pp.439-454.

Mitani, J.C. and Watts, D.P. (2001) Why do chimpanzees hunt and share meat?, *Animal behavior*, vol.61, pp.915-924.

Moodie, R. L. (1918) Studies in paleopathology. III. Opisthotonus and allied phenomena among fossil vertebrates, *American Naturalist*, vol.52, pp.384-394.

Moodie, R.L. (1923) *Paleopathology: An Introduction to the Study of Ancient Evidences of Disease*. University of Illinois Press: Urbana.

Morey, D.F. and Klippel, W.E. (1991) Canid scavenging and deer bone survivorship at an archaic period site in Tennessee, *Archaeozoologia*, vol.4, no.1, pp.11-28.

Morlan, R.E. (1984) Toward the definition of criteria for the recognition of artificial bone alterations, *Quaternary Research*, vol.22, pp.160-171.

Morse, D., Crusoe, D. and Smith, H.G. (1976) Forensic archaeology, *Journal of Forensic Sciences*, vol.21, no.2, pp.323-332.

Mucina, L. and Rutherford, M.C., eds. (2006) The vegetation of South Africa, Lesotho and Swaziland. *Strelitzia*, vol.19: Pretoria, South African National Biodiversity Institute.

Müller, A. H. (1951) Grundlagen der Biostratonomie, *Deutsche Akademie der Wissenschaften zu Berlin, Abhandlungen*, vol.3, pp.1-146.

Murphy, W.A., zur Nedden, D., Gostner, P., Knapp, R., Recheis, W. and Seidler, H. (2003) The iceman: discovery and imaging, *Radiology*, vol.226, no.3, pp.614-629.

Mutter, R.J, Berger, L.R. and Schmid, P. (2001) New evidence of the giant hyaena, *Pachycrocuta brevirostris* (Carnivora: Hyaenidae), from the Gladysvale Cave Deposit (Plio-Pleistocene, John Nash Nature Reserve, Gauteng, South Africa), *Palaeontologia Africana*, vol.37, pp.103-113.

Myers, T.P., Voorhies, M.R. and Corner, R.G. (1980) Spiral fractures and bone pseudotools at paleontological sites, *American Antiquity*, vol.45, no.3, pp.483-490.

Newman, R.A. (1993) The incidence of damage marks on Swartkrans fossil bones from the 1979-1986 excavations, In: Brain, C.K. (ed.) *Swartkrans: A Cave's Chronicle of Early Man*, pp.217-228. Transvaal Museum Monograph No.8: Pretoria.

Newton-Fischer, N.E., Notman, H. and Reynolds, V. (2002) Hunting of mammalian prey by Budongo Forest chimpanzees, *Folia Primatologica*, vol.73, no.5, pp.281-283.

Nicholson, R.A. (1992) Bone survival: the effects of sedimentary abrasion and trampling on fresh and cooked bone, *International Journal of Osteoarchaeology*, vol.2, pp.79-90.

Nigro, J.D., Ungar, P.S., de Ruiter, D.J. and Berger, L.R. (2003) Developing a Geographical Information System (GIS) for mapping and analysing fossil deposits at Swartkrans, Gauteng Province, South Africa, *Journal of Archaeological Science*, vol.30, pp.317-324.

Nishida, T., Hiraiwa-Hasegawa, M., Hasegawa, T. and Takahata, Y. (1985) Group extinction and female transfer in wild chimpanzees in the Mahale National Park, Tanzania, *Zeitschrift für Tierpsychologie*, vol.67, no.1-4, pp.284-301.

Njau, J.K. and Blumenschine, R.J. (2006) A diagnosis of crocodile feeding traces on larger mammal bone, with fossil examples from the Plio-Pleistocene Olduvai Basin, Tanzania, *Journal of Human Evolution*, vol. 50, pp.142-162.

Novecovsky, B.J. and Popkin, P.R.W. (2005) Canidae volume bone mineral density values: an application to sites in western Canada, *Journal of Archaeological Science*, vol.32, pp.1677-1690.

O'Brien, T.G. and Kuehner, A.C. (2007) Waxing grave about adipocere: soft tissue change in an aquatic context, *Journal of Forensic Sciences*, vol.52, no.2, pp.294-301.

Ochev, V.G. (1995) Mysterious Kotel'nich, *Priroda*, vol.2, pp.53-59.

Oliver, J. S. (1984). Bone morphologies from Shield Trap Cave, Carbon County, Montana, *Abstracts of the First International Conference on Bone Modification*, p.27. Carson City, Nevada, August 17-19, 1984.

Oliver, J. S. (1986) The Taphonomy and Paleoecology of Shield Trap Cave (24CB91), Carbon County, Montana, M.S. thesis, University of Maine, Orono.

Oliver, J.S. (1994) Estimates of hominid and carnivore involvement in the FLK *Zinjanthropus* fossil assemblage: some socioecological implications, *Journal of Human Evolution*, vol.27, pp.267-294.

Olsen, S.L. and Shipman, P. (1988) Surface modification on bone: trampling versus butchery, *Journal of Archaeological Science*, vol.15, pp.535-553.

O'Regan, H.J. and Menter, C.G. (2009) Carnivore from the Plio-Pleistocene hominin site of Drimolen, Gauteng, South Africa, *Geobios*, vol.42, pp.329-350.

O'Regan, H.J. and Reynolds, S.C. (2009) An ecological reassessment of the southern African carnivore guild: a case study from Member 4, Sterkfontein, South Africa, *Journal of Human Evolution,* vol.57, pp.212-222.

Partridge, T. C. (2000) Hominid-bearing cave and tufa deposits, In: Partridge, T.C. and Maud, R.R. (eds.) *The Cenozoic of Southern Africa*, pp. 100-130. Oxford University Press: Oxford.

Partridge, T.C., Granger, T.C., Caffee, M.W. and Clarke, R.J. (2003) Lower Pliocene hominid remains from Sterkfontein, *Science*, vol.300, pp.607-612.

Payne, J.A. (1965) A summer carrion study of the baby pig *Sus scrofa* Linnaeus, *Ecology*, vol.46, pp.592-602.

Payne, J.A. and King, E.W. (1970) Coleoptera associated with pig carrion, *Entomologist's Monthly Magazine*, vol.105, pp.224-232.

Payne, J.A. and King, E.W. (1972) Insect succession and decomposition of pig carcasses in water, *Journal of the Georgia Entomological Society*, vol.7, pp.153-162.

Payne, J.A., King, E.W. and Beinhart, G. (1968) Arthropod succession and decomposition of buried pigs, *Nature*, vol.219, pp.1180-1181.

Payne, S. (1975) Partial recovery and sample bias, In: Clason, A.T. (ed.) *Archaeozoological Studies*, North Holland, Amsterdam, pp.7-17.

Peabody, F.E. (1954) Travertines and cave deposits of the Kaap escarpment of South Africa, and the type locality of *Australopithecus africanus* Dart, *Bulletin of the Geological Society of America*, vol.65, pp.671-706.

Pei, W.C. (1938) Le rôle des animaux et des causes naturelles dans la cassure des os, *Palaeontologia Sinica*, vol.7, pp.1-16.

Pettitt, P. (2011) *The Palaeolithic Origins of Human Burial*. Routlegde : New York.

Pickering, R. (2005) The Stratigraphy, Chronology and Palaeoenvironment of the Pleistocene Cave Fill, Gladysvale Cave, South Africa, M.Sc. thesis, University of the Witwatersrand, Johannesburg.

Pickering, R., Hancox, P.J., Lee-Thorp, J.A., Grün, R., Mortimer, G.E., McCulloch, M. and Berger, L.R. (2007) Stratigraphy, U-Th chronology, and paleoenvironments at Gladysvale Cave: insights into the climatic control of South African hominin-bearing cave deposits, *Journal of Human Evolution*, vol.53, pp.602-619.

Pickering, R., Dirks, P.H.G.M., Jinnah, Z., de Ruiter, D.J., Churchil, S.E., Herries, A.I.R., Woodhead, J.D., Hellstrom, J.C. and Berger, L.R. (2011) *Australopithecus sediba* at 1.977 Ma and implications for the origins of the genus *Homo*, *Science*, vol.333, pp.1421-1423.

Pickering, T.R. (1999) Taphonomic Interpretations of the Sterkfontein Early Hominid Site (Gauteng, South Africa) Reconsidered in Light of Recent Evidence, Ph.D. thesis, University of Wisconsin, Madison.

Pickering, T.R. (2001a) Taphonomy of the Swartkrans hominid post-crania and its bearing on issues of meat-eating and fire management, In: Stanford, C.B., Bunn, H.T. (eds.) *Meat-Eating and Human Evolution*, pp.31-51. Oxford University Press: Oxford.

Pickering, T.R. (2001b) Carnivore voiding; a taphonomic process with the potential for the deposition of forensic evidence, *Journal of Forensic Science*, vol.46, pp.406-411.

Pickering, T.R. (2002) Reconsideration of criteria for differentiating faunal assemblages accumulated by hyaenas and hominids, *International Journal of Osteoarchaeology*, vol.12, pp.127-141.

Pickering, T.R. and Wallis, J. (1997) Bone modifications resulting from captive chimpanzee mastication: implications for the interpretation of Pliocene archaeological faunas, *Journal of Archaeological Science*, vol.24, pp.1115-1127.

Pickering, T.R., White, T. and Toth, N. (2000) Brief Communication: cutmarks on a Plio-Pleistocene hominid from Sterkfontein, South Africa, *American Journal of Physical Anthropology*, vol.111, pp.579-584.

Pickering, T.R. and Carlson, K.J. (2004) Baboon taphonomy and its relevance to the investigation of large felid involvement in human forensic cases, *Forensic Science International*, vol.144, pp.37-44.

Pickering, T.R. Clarke, R.J. and Heaton, J.L. (2004a) The context of Stw 573, an early hominid skull and skeleton from Sterkfontein Member 2: taphonomy and paleoenvironment, *Journal of Human Evolution*, vol.46, pp.279-297.

Pickering, T.R., Clarke, R.J. and Moggi-Cecchi, J. (2004b) The role of carnivores in the accumulation of the Sterkfontein Member 4 hominid assemblage: a taphonomic reassessment of the complete hominid fossil sample (1936-1999), *American Journal of Physical Anthropology*, vol.125, pp.1-15.

Pickering, T.R., Domínguez -Rodrigo, M., Egeland, C.P. and Brain, C.K. (2004c) Beyond leopards: tooth marks and the contribution of multiple carnivore taxa to the accumulation of the Swartkrans Member 3 fossil assemblage, *Journal of Human Evolution*, vol.46, pp.595-604.

Pickering, T.R., Domínguez -Rodrigo, M., Egeland, C.P. and Brain, C.K. (2004d) New data and ideas on the foraging behaviour of Early Stone Age hominids at Swartkrans Cave, South Africa, *South African Journal of Science*, vol.100, pp.215-219.

Pickford, M. and Senut, B. (2001) The geological and faunal context of Late Miocene hominid remains from Lukeino, Kenya, *Earth and Planetary Sciences*, vol.332, pp.145-152.

Plug, C. and Plug, I. (1990) MNI counts as estimates of species abundance, *The South African Archaeological Bulletin*, vol.45, no.151, pp.53-57.

Plug, I. and Keyser, A.W. (1994) Haasgat Cave, a Pleistocene site in the central Transvaal: geomorphological, faunal and taphonomic considerations, *Annals of the Transvaal Museum*, vol.36, pp.139-145.

Pobiner, B. L., DeSilva, J., Sanders, W.J. and Mitani, J.C. (2007) Taphonomic analysis of skeletal remains from chimpanzee hunts at Ngogo, Kibale National Park, Uganda, *Journal of Human Evolution*, vol.52, pp.614-636.

Pomi, L.H. and Tonni, E.P. (2011) Termite traces on bones from the Late Pleistocene of Argentina, *Ichnos: An International Journal for Plant and Animal Traces*, vol.18, no.3, pp.166-171.

Potts, R. (1988) *Early Hominid Activities at Olduvai Gorge*. Aldine de Gruyter: New York.

Potts, R. and Shipman, P. (1981) Cutmarks made by stone tools on bones from Olduvai Gorge, Tanzania, *Nature*, vol.291, pp.577-590.

Prado e Castro, C.P., Sousa, J.P., Arnaldos, M.I., Gaspar, J. and García, M.D. (2011) Blowflies (Diptera: Calliphoridae) activity in the sun exposed and shaded carrion in Portugal, *Annales de la Société Entomologique de France*, Nouvelle série, vol.47, no.1-2, pp.128-139.

Pruetz, J.D. (2007) Evidence of cave use by savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal: implications for thermoregulatory behavior, *Biomedical and Life Science*, vol.48, pp.316-319.

Quan, Z. and Wei-de, J. (1995) First report on studying dinosaur egg fossils with methods of medical CT scanning, *Acta Palaeontologica Sinica*, vol.34, no.6, pp.777-779.

Radosevich, S.C., Retallack, G.J., and Taieb, M. (1992) Reassessment of the paleoenvironment and preservation of hominid fossils from Hadar, Ethiopia, *American Journal of Physical Anthropology*, vol.87, pp.15-27.

Reed K.E. (1996) The Paleoecology of Makapansgat and Other African Plio-Pleistocene Hominid Localities, Ph.D. thesis, University of New York, Stony Brook.

Reisdorf, A.G. and Wuttke, M. (2012) Re-evaluating Moddie's opisthotonic-posture hypothesis in fossil vertebrates. Part I: Reptiles – the taphonomy of the bipedal dinosaurs *Compsognathus longipes* and *Juravenator starki* from the Solnhofen Archipelago (Jurassic, Germany), *Palaeobiodiversity and Palaeoenvironments*, vol.92, pp.119-168.

Reynolds, S.C. (2010) Where the wild things were: spatial and temporal distribution of carnivores in the Cradle of Humankind (Gauteng, South Africa) in relation to the accumulation of mammalian and hominin assemblages, *Journal of Taphonomy*, vol.8, no.1-2, pp.233-257.

Reynolds, S.C. and Kibii, J.M. (2011) Sterkfontein at 75: review of palaeoenvironments, fauna and archaeology from the hominin site of Sterkfontein (Gauteng Province, South Africa), *Palaeontologia Africana*, vol.46, pp.59-88.

Reynolds, S.C., Vogel, J.C., Clarke, R.J. and Kuman, K.A. (2003) Preliminary results of excavations at Lincoln Cave, Sterkfontein, South Africa, *South African Journal of Science*, vol.99, pp.286-288.

Reynolds, S.C., Clarke, R.J. and Kuman, K.A. (2007) The view from the Lincoln Cave: mid- to late Pleistocene fossil deposits from Sterkfontein hominid site, South Africa, *Journal of Human Evolution*, vol.53, pp.260-271.

Reynolds, S.C., Bailey, G.N. and King, G.C.P. (2011) Landscapes and their relation to hominin habitats: case studies from *Australopithecus* sites in eastern and southern Africa, *Journal of Human Evolution*, vol.60, pp.281-298.

Richardson, P.R.K. (1980) Carnivore damage to antelope bones and its archaeological implications, *Palaeontologia Africana*, vol.23, pp.109-125.

Rigaud, J-P. and Simek, J. (1991) Interpreting spatial patterns at Grotte XV: a multiple-method approach, In: Kroll, E.M. and Douglas Price, T. (eds.) *The Interpretation of Archaeological Spatial Patterning,* pp. 199-220. Plenum Press: New York.

Rixon, A.E. (1949) The use of acetic and formic acids in the preparation of fossil vertebrates, *Museum Journal London*, vol.49, pp.116-117.

Robert, I. and Vigne, J.-D. (2002a) The bearded vulture (*Gypaetus barbatus*) as an accumulator of archaeological bones. Late glacial assemblages and present-day reference data in Corsica (Western Mediterranean), *Journal of Archaeological Science*, vol.29, pp.763-777.

Robert, I. and Vigne, J.-D. (2002b) Bearded vulture *Gyp*. *barbatus* contributions to the constitution of two different bone assemblages: modern reference data and an archaeological example in Corsica, *Acta zoologica cracoviensa*, vol.45, pp.319-329.

Roberts, E.M., Rogers, R.R. and Foreman, B.Z. (2007) Continental insect borings in dinosaur bone: examples from the late Cretaceous of Madagascar and Utah, *Journal of Paleontology*, vol.81, no.1, pp.201-208.

Robinson, J.T. (1953) The nature of *Telanthropus capensis*, *Nature*, vol.171, p.33.

Robinson, J.T. (1961) The australopithecines and their bearing on the origin of Man and of stone tool making, *South African Journal of Science*, vol.57, pp.3-16.

Rodriguez, W.C. and Brass, W.M. (1985) Decomposition of buried bodies and methods that may aid in their location, *Journal of Forensic Science*, vol.30, no.3, pp.836-852.

Rogers, R.R. (1990) Taphonomy of three dinosaur bone beds in the Upper Cretaceous Two Medicine Formation of Northwestern Montana: evidence for drought-related mortality, *PALAIOS*, vol.5, no.5, pp.394-413.

Rogers, R.R., Eberth, D.A., and Fiorillo, A.R. eds (2007) *Bonebeds, Genesis, Analysis, And Paleobiological Significance*. The University of Chicago Press: Chicago.

Roksandic, M. (2002) Position of skeletal remains as a key to understanding mortuary behaviours, In: Haglund, W.D. and Sorg, M.H. (eds.) *Advances in Forensic Taphonomy: Method, Theory and Archaeological Perspectives*, pp.99-117. Boca Raton (FL): CRC Press.

Rosell, C., Prenández-Llario, P. and Herrero, J. (2001) El Jabalí ("*Sus scrofa* LINNAEUS", 1758), *Galemys*, vol.13, no.2, pp.1-25.

Rudner, I. (1970) On how to prepare a fossil – A guide for beginners, *South African Museum Association Bulletin*, vol.9, no.12, pp.402-408.

Rudner, I. (1972) Preparing fossils with acid – A step-by-step account, *Curator: the Museum Journal*, vol.15, no.2, pp.121-130.

Ruff, C. (2008) Femoral/humeral strength in early African *Homo erectus*, *Journal of Human Evolution*, vol.54, pp.383-390.

Saladié, P. (2009) Experimental Chewing and Gnawing of Humans and Other Primates Compared to Canids, Suids and Felids, Ph.D. thesis, University Rovira i Virgili, Tarragona.

Sanders, W.J., Trapani, J. and Mitani, J.C. (2003) Taphonomic aspects of crowned hawk-eagle predation on monkeys, *Journal of Human Evolution*, vol.44, pp.87-105.

Saneyoshi, M., Watabe, M., Suzuki, S. and Tsogtbaatar, K. (2011) Trace fossils on dinosaur bones from Upper Cretaceous eolian deposits in Mongolia: taphonomic interpretations of paleoecosystems in ancient desert environments, *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol.311, pp.38-47.

Sandgathe, D.M., Dibble, H.L., Goldberg, P. and McPherron, S.P. (2011) The Roc de Marsal Neandertal child: a reassessment of its status as a deliberate burial, *Journal of Human Evolution*, vol.61, pp.243-253.

Sarna-Wojcicki, A.M., Meyer, C.E., Roth, P.H. and Brown, F.H. (1985) Ages of tuff beds at East African early hominid sites and sediments in the Gulf of Aden, *Nature*, vol.313, pp.306-308.

Sawada, Y., Pickford, M., Senut, B., Itaya, T., Hyodo, M., Miura, T., Kashine, C., Chujo, T. and Fujii, H. (2002) The age of *Orrorin tugenensis*, an early hominid from the Tugen Hills, Kenya. *Comptes Rendus Palevol*, vol.1, pp.293-303.

Schotsmans, E.M.J., Denton, J., Dekeirsschieter, J., Ivaneanu, T., Leentjes, S., Janaway, R.C. and Wilson, A.S. (2012) Effects of hydrated lime and quicklime on the decay of buried human remains using pig cadavers as human body analogues, *Forensic Science International*, vol.217, pp.50-59.

Scott, L. and Rossouw, L. (2005) Reassessment of botanical evidence for palaeoenvironments at Florisbad, Sout Africa, *South African Archaeological Bulletin*, vol.60, no.182, pp.96-102.

Seilacher, A., Reif, W.-E. and Westphal, F. (1985) Sedimentological, ecological and temporal patterns of fossil Lagerstätten, *Philosophical Transactions of the Royal Society of London*, vol.311, pp.5-23.

Selvaggio, M.M. (1994a) Evidence from Carnivore Tooth Marks and Stone-Tool-Butchery Marks for Scavenging by Hominids at FLK *Zinjanthropus*, Olduvai Gorge, Tanzania, Ph.D. thesis, Rutgers University, New Brunswick.

Selvaggio, M.M. (1994b) Carnivore tooth marks and stone tool butchery marks on scavenged bones: archaeological implications, *Journal of Human Evolution*, vol.27, pp.215-228.

Selvaggio, M.M. (1998) Evidence for a three-stage sequence of hominid and carnivore involvement with long bones at FLK *Zinjanthropus*, Olduvai Gorge, Tanzania, *Journal of Archaeological Science*, vol.25, pp.191-202.

Selvaggio, M.M. and Wilder, J. (2001) Identifying the involvement of multiple carnivore taxa with archaeological bone assemblages, *Journal of Archaeological Science*, vol.28, pp.465-470.

Sénégas, F. and Avery, M. (1998) New evidence for the murine origins of the Otomyinae (Mammalia, Rodentia) and the age of Bolt's Farm (South Africa), *South African Journal of Science*, vol.94, pp.503-507.

Senut, B., Pickford, M., Gommery, D., Mein, P., Cheboi, K. and Coppens, Y. (2001) First hominid from the Miocene (Lukeino Formation, Kenya), *Earth and Planetary Sciences*, vol.332, pp.137-144.

Seydack, A.H.W. (1990) Ecology of the Bushpig *Potamochoerus porcus* Linn. 1758 in the Cape Province, South Africa, Ph.D thesis, University of Stellenbosch.

Shäfer, W. (1972) *Aktuo-Palaiontologie nach Studien in der Nordsee*. Waldemar Kramer: Frankfurt am Main.

Shaller, G.B. (1972) *The Serengeti Lion: a Study of Predator-Prey Relations*. University of Chicago Press: Chicago.

Sharanowski, B.J., Walker, E.G. and Anderson, G.S. (2008) Insect succession and decomposition patterns on shaded and sunlit carrion in Saskatchewan in three different seasons, *Forensic Science International*, vol.179, pp.219-240.

Shean, B.S., Messinger, L. and Papworth, M. (1993) Observations of differential decomposition on sun exposed v. shaded pig carrion in coastal Washington State, *Journal of Forensic Sciences*, vol.38, no.4, pp.938-949.

Shin, D.H., Choi, Y.H., Shin, K.-J., Han, G.R., Youn, M., Kim, C.-Y., Han, S.H., Seo, J.C., Park, S.S., Cho, Y.-J. and Chang, B.S. (2003) Radiological analysis on a mummy from a medieval tomb in Korea, *Annals of Anatomy*, vol.185, pp.377-382.

Shin, M.H., Yi, Y.S., Bok, G.D., Lee, E., Spigelman, M. and Shin, D.H. (2008) How did mummification occur in bodies buried in tombs with a lime soil mixture barrier during the Joseon Dynasty in Korea, In: Peńa, P.A., Martín, R.M. and Rodríguez, A.R. (eds.) *Mummies and Science World Mummies Research*: Santa Cruz de Tenerife, VI World Congress on Mummy Studies, pp.105-113.

Shipman, P. (1975) Implications of drought for vertebrate fossil assemblages, *Nature*, vol.257, pp.667-668.

Shipman, P. (1981a) *Life History of a Fossil, an Introduction to Taphonomy and Paleoecology*. Harvard University Press: Cambridge, Mass.

Shipman, P. (1981b) Applications of scanning electron microscopy to taphonomic problems, *Annals of the New York Academy of Sciences*, vol.376, no.1, pp.357-385.

Shipman, P. (1989) Altered bones from Olduvai Gorge, Tanzania: Techniques, problems, and implications of their recognition, In: Bonnichsen, R. and Sorg, M.H. (eds.) *Bone Modification*, pp.317-334. Orono: University of Maine Centre for the Study of the First Americans, Thompson-Shore Inc. USA.

Shipman, P. and Phillips-Conroy, J.E. (1976) On scavenging by hominids and other carnivores. *Current Anthropology*, vol.17, pp.170-173.

Shipman, P. and Phillips-Conroy, J.E. (1977) Hominid tool-making versus carnivore scavenging, *American Journal of Physical Anthropology*, vol.46, pp.77-86.

Shipman, P., Bosler, W., Lee Davis, K., Behrensmeyer, A.K., Dunbar, R.I.M., Groves, C.P., Thackeray, F., Harris Van Couvering, J. and Stucky, R.K. (1981) Butchery on giant geladas at an Acheulian site [and comments and reply], *Current Anthropology*, vol.22, no.3, pp.257-268.

Shipman, P. and Rose, J. (1983a) Early hominid hunting, butchering, and carcass-processing behaviors: approaches to the fossil record, *Journal of Anthropological Archaeology*, vol.2, pp.57-98.

Shipman, P. and Rose, J. (1983b) Evidence of butchery and hominid activities at Torralba and Ambrona; an evaluation using microscopic techniques, *Journal of Archaeological Science*, vol.10, pp.465-474.

Shipman, P. and Rose, J. (1988) Bone tools: an experimental approach, In: Olsen, S. (ed.) *Scanning Electron Microscopy in Archaeology*, British Archaeological Reports International Series, vol.452, pp.303-335: Oxford.

Sillen, A. (1992) Strontium-calcium ratios (Sr/Ca) of *Australopithecus robustus* and associated fauna from Swartkrans, *Journal of Human Evolution*, vol.23, pp.495-516.

Sillen, A., Hall, G. and Armstrong, R. (1995) Strontium calcium ratios (Sr/Ca) and strontium isotopic ratios ($^{87}Sr/^{86}Sr$) of *Australopithecus robustus* and *Homo* sp. from Swartkrans, *Journal of Human Evolution*, vol.28, pp.277-285.

Simmons, T., Cross, P.A., Adlam, R.E. and Moffatt, C. (2010a) The influence of insects on decomposition rate in buried and surface remains, *Journal of Forensic Sciences*, vol.55, no.4, pp.889-892.

Simmons, T., Adlam, R.E. and Moffatt, C. (2010b) Debugging decomposition data – comparative taphonomic studies and the influence of insects and carcass size on decomposition rate, *Journal of Forensic Sciences*, vol.55, no.1, pp.1-6.

Simons, J. (1966) The presence of leopard and a study of the food debris in the leopard lairs of the Mount Suswa Caves, Kenya, *Bulletin of the Cave Exploration Group of East Africa*, vol.1, pp.51-69.

Skinner, J.D. and van Aarde, R.J. (1991) Bone collecting by brown hyaenas *Hyaena brunnea* in the Central Namib Desert, Namibia, *Journal of Archaeological Science*, vol.18, pp.513-523.

Skinner, J. D. and Chimimba, C.T. (2005) *The Mammals of the Southern African Subregion*. Cambridge University Press.

Smilg, J.S. (2012) Application of CT imaging technologies to fossil-bearing rocks from South African early hominin sites, Ph.D. thesis, University of the Witwatersrand, Johannesburg.

Smirnov, Y. (1989) Intentional human burial: Middle Paleolithic (Last Glaciation) beginnings, *Journal of World Prehistory*, vol.3, no.2, pp.199-233.

Smith, R.M.H. (1980) The lithology, sedimentology and taphonomy of flood-plain deposits of the Lower Beaufort (Adelaide Subgroup) strata near Beaufort West, *Transactions of the Geological Society of South Africa*, vol.83, pp.399-413.

Smith, R.M.H. (1987) Helical burrow casts of therapsid origin from the Beaufort Group (Permian) of South Africa, *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol.60, pp.155-170.

Smith, R.M.H. (1993) Vertebrate taphonomy of late Permian floodplain deposits in the southwestern Karoo Basin of South Africa, *PALAIOS*, vol.8, no.1, pp.45-67.

Smith, R.M.H. (1995) Changing fluvial environments across the Permian-Triassic boundary in the Karoo Basin, South African and possible causes of tetrapod extinctions, *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol.117, pp.81-104.

Smith, R.M.H. and Evans, S.E. (1996) New material of *Youngina*: evidence of juvenile aggregation in Permian diapsid reptiles, *Palaeontology*, vol.39, part.2, pp.289-303.

Smith, R.M.H. and Ward, P.D. (2001) Pattern of vertebrate extinctions across an event bed at the Permian-Triassic boundary in the Karoo Basin of South Africa, *Geology*, vol.29, pp.1147-1150.

Smith, K.G.V. (1986) *A Manual of Forensic Entomology*. British Museum of Natural History and Cornell University Press.

Snow, C.C. (1982) Forensic anthropology, *Annual Review of Anthropology*, vol.11, pp.97-131.

Sponheimer, M. and Lee-Thorp, J.A. (1999) Isotopic evidence for the diet of an early hominid, *Australopithecus africanus*, *Science*, vol.283, pp.368-369.

Sponheimer, M., de Ruiter, D.J., Lee-Thorp, J.A. and Späth, A. (2005) Sr/Ca and early hominin diets revisited: new data from modern and fossil tooth enamel, *Journal of Human Evolution*, vol.48, pp.147-156.

Sponheimer, M., Passey, B.H., de Ruiter, D.J. Guatelli-Steinberg, D., Cerling, T.E. and Lee-Thorp, J.A. (2006) Isotopic evidence for dietary variability in the early hominin *Paranthropus robustus*, *Science*, vol.314, pp.980-982.

Stallibrass, S. (1984) The distinction between the effects of small carnivores and humans on post-glacial faunal assemblages. A case study using scavenging faunal assemblages, In: Grigson, C. and Clutton-Brock, J. (eds.) *Animal and Archaeology, 4: Husbandry in Europe*, British Archaeological Reports International Series, vol.227, pp.259-269 : Oxford.

Stanford, R., Weishampel, D.B. and Deleon, V.B. (2011) The first hatchling dinosaur reported from the eastern United States: *Propanoplosaurus marylandicus* (Dinosauria: Ankylosauria) from the early Cretaceous of Maryland, U.S.A., *Journal of Paleontology*, vol.85, no.5, pp.916-924.

Steininger, C.M. (2010) The Dietary Behaviour of Early Pleistocene Bovids from Cooper's Cave and Swartkrans, South Africa, Ph.D. thesis, University of the Witwatersrand, Johannesburg.

Stiner, M.C. (1991) Food procurement and transport by human and non-human predators, *Journal of Archaeological Science*, vol.18, pp.455-482.

Susman, R.L. and Stern, J.T. (1982) Functional morphology of *Homo habilis*, *Science*, vol.217, pp.931-934.

Sutcliffe, A.J. (1970) Spotted hyaena: crusher, gnawer, digester, and collector of bones, *Nature*, vol.227, pp.1110-1113.

Sutcliffe, A. J. (1973) Caves of the east African Rift Valley, *Transactions of the Cave Research Group of Great Britain*, vol.15, pp.41-65.

Tappen, M. and Wrangham, R. (2000) Recognizing hominoid-modified bones: the taphonomy of *Colobus* bones partially digested by free-ranging chimpanzees in the Kibale Forest, Uganda, *American Journal of Physical Anthropology*, vol.113, pp.217-234.

Teleki, G. (1973a) *The Predatory Behavior of Wild Chimpanzees*. Lewisburg (PA): Bucknell University.

Teleki, G. (1973b) The omnivorous chimpanzee, *Scientific American*, vol.228, pp.32-42.

Texier, J.-P. (2000) À propos des processus de formation des sites préhistoriques, *PALEO*, vol.12, pp.379-389.

Thackeray, J.F., Gommery, D., Sénégas, F., Potze, S., Kgasi, L., McCrae, C. and Prat, S. (2008) A survey of past and present work on Plio-Pleistocene deposits on Bolt's Farm, Cradle of Humankind, South Africa, *Annals of the Transvaal Museum*, vol.45, pp.83-89.

Thorne, B.L. and Kimsey, R.B. (1983) Attraction of neotropical *Nasutitermes* termites to carrion, *Biotropica*, vol.15, no.4, pp.295-297.

Tobien, H. (1965) Insekten-Fraßspuren an tertiaren und pleistozanen Saugetier-Knochen, *Senckenbergiana Lethaea*, vol.46a, pp.441-451.

Toombs, H. A. (1948) The use of acetic acid in the development of vertebrate fossils, *The Museum Journal*, vol. 48, pp. 54-55.

Toombs, H.A., and Rixon, A.E. (1959) The use of acids in the preparation of vertebrate fossils, *Curator: The Museum Journal*, vol.2, no.4, pp.304-312.

Toots, H. (1965) Sequence of disarticulation in mammalian skeletons, *University of Wyoming Contributions to Geology*, vol.4, pp.37-39.

Trapani, J., Sanders, W.J., Mitani, J.C., Heard, A., (2006) Precision and consistency of the taphonomic signature of predation by crowned hawk-eagles (*Stephanoaetus coronatus*) in Kibale National Park, Uganda, *PALAIOS*, vol.21, pp.114-131.

Trinkaus, E. (1985) Cannibalism and burial at Krapina, *Journal of Human Evolution*, vol.14, pp.203-216.

Turner, A. (1987a) *Megantereon cultridens* (Cuvier) (Mammalia, Felidae, Machairodontinae) from Plio-Pleistocene deposits in Africa and Eurasia, with comments on dispersal and the possibility of a New World Origin, *Journal of Paleontology*, vol.61, pp. 1256-1268.

Turner, A. (1987b) New fossil carnivore remains from the Sterkfontein hominid site (Mammalia: Carnivora), *Annals of the Transvaal Museum*, vol.34, no.15, pp.319-347.

Turner, A. (1997) Further remains of Carnivora (Mammalia) from the Sterkfontein hominid site, *Palaeontologia africana*, vol.34, pp.115-126.

Turner, A. (2004) New fossil carnivore remains from Swartkrans, In: Brain, C.K. (ed.) *Swartkrans, A Cave's Chronicle of Early Man*, pp.151-165. Transvaal Museum Monograph No.8: Pretoria.

Turner, B. and Wiltshire, P. (1999) Experimental validation of forensic evidence: a study of the decomposition of buried pigs in a heavy clay soil, *Forensic Science International*, vol.101, pp.113-122.

Ubelaker, D.H. (1997) Taphonomic applications in forensic anthropology, In: Haglund, W.D. and Sorg, M.H. (eds.) *Forensic Taphonomy: The Postmortem Fate of Human Remains*, pp.77-90. CRC Press, Boca Raton, FL: USA.

Ubelaker, D.H. and Hunt, D.R. (1995) The influence of William M. Bass III on the development of American forensic anthropology, *Journal of Forensic Sciences*, vol.40, pp.729-734.

Uehara, S. (1997) Predation by the Chimpanzee (*Pan troglodytes*), *Primates*, vol.38, no.2, pp.193-214.

Ungar, P. (2004) Dental topography and diets of *Australopithecus afarensis* and early *Homo*, *Journal of Human Evolution*, vol.46, pp.605-622.

van der Merwe, N.J., Thackeray, J.F., Lee-Thorp, J.A. and Luyt, J. (2003) The carbon isotope ecology and diet of *Australopithecus africanus* at Sterkfontein, South Africa, *Journal of Human Evolution*, vol.44, pp.581-597.

Val, A., Carlson, K.J., Steininger, C., Kibii, J.M., Churms, C., Kuhn, B.F. and Berger, L.R. (2011) 3D techniques and fossil identification: an elephant shrew mandible from the Malapa site, *South African Journal of Science*, vol.107, no.11-12, pp.1-5.

Val, A., Steininger, C. and Taru, P. (in prep.) Where are the hominins? The primate taphonomy at Cooper's D.

Vass, A.A. (2001) Beyond the grave – understanding human composition, *Microbiology Today*, vol.28, pp.190-192.

Vass, A.A., Bass, W.M., Wolt, J.D., Foss, J.E. and Ammons, J.T. (1992) Time since death determinations of human cadavers using soil solution, *Journal of Forensic Sciences*, vol.37, no.5, pp.1236-1253.

Vignaud, P., Duringer, P., Mackaye, H.T., Likius, A., Blondel, C., Boisserie, J.-R., de Bonis, L., Eisenmann, V., Etienne, M.-E., Geraads, D., Guy, F., Lehmann, T., Lihoreau F., Lopez-Martinez, N., Mourer-Chauviré, C., Otero, O., Rage, J.-C., Schuster, M., Viriot, L., Zazzo, A. and Brunet, M. (2002) Geology and palaeontology of the Upper Miocene Toros-Menalla hominid locality, Chad, *Nature*, vol.418, pp.152-155.

Villa, P. (1989) On the evidence for Neandertal burial, *Current Anthropology*, vol.30, no.3, pp.322-330.

Villa, P (1992) Cannibalism in prehistoric Europe, *Evolutionary Anthropology*, vol.1, no.3, pp.93-104.

Villa, P. and Mahieu, E. (1991) Breakage patterns of human long bones, *Journal of Human Evolution*, vol.21, pp.27-48.

Villa, P. and Bartram, L. (1996) Flaked bone from a hyena den, *Paléo*, vol.8, pp.143-159.

Villa, P., Bouville, C., Courtin, J., Helmer, D., Mahieu, E., Shipman, P., Belluomini, G. and Branca, M. (1986) Cannibalism in the Neolithic, *Science*, vol.233, pp.431-437.

von Hoermann, C., Ruther, J. and Ayasse, M. (2012) The attraction of virgin female hide beetles (*Dermestes maculatus*) to cadavers by a combination of decomposition odour and male sex pheromones, *Frontiers in Zoology*, vol.9, pp.1-10.

Voorhies, M.R. (1966) Taphonomy and Population Dynamics of an Early Pliocene Vertebrate Fauna, Knox County, Nebraska, Ph.D. thesis, University of Wyoming, Laramie.

Voorhies, M.R. (1969) Taphonomy and population dynamics of an early Pliocene vertebrate fauna, Know County, Nebraska, *University of Wyoming Contributions to Geology* Special Paper, vol.1, pp.1-6.

Vrba, E.S. (1975) Some evidence of chronology and palaeoecology of Sterkfontein, Swartkrans and Kromdraai from the fossil Bovidae, *Nature*, vol.254, pp.301-304.

Vrba, E.S. (1980) The significance of bovid remains as indicators of environment and predation patterns, In: Behrensmeyer, A.K. and Hill, A. (eds.) *Fossils in the Making*, pp.247-271. University Chicago Press: Chicago.

Walker, A. (1993) Chapter 4, taphonomy, In: Walker, A. and Leakey, R. (eds.) *The Nariokotome* Homo erectus *Skeleton*, pp.40-53. Harvard University Press: Cambridge, MA.

Watson, J.A.L. and Abbey, H.M. (1986) The effects of termites (*Isoptera*) on bone: some archaeological implications, *Sociobiology*, vol.11, no.3, pp.245-253.

Watson, V. (1993) Composition of the Swartkrans bone accumulations, in terms of skeletal parts and animals represented, In: Brain, C.K. (ed.) *Swartkrans, A Cave's Chronicle of Early Man*, pp.35-73. Transvaal Museum Monograph No.8: Pretoria.

Watts, D.P. and Mitani, J.C. (2001) Boundary patrols and intergroup encounters in wild chimpanzees, *Behaviour*, vol.138, pp.299-327.

Watts, D.P., Muller, M., Amsler, S.J., Mbabazi, G. and Mitani, J.C. (2006) Lethal intergroup aggression by chimpanzees in Kibale National Park, Uganda, *American Journal of Primatology*, vol.68, pp.161-180.

Weichbrod, R.H. (1987) The Dermestid Beetle: a tiny laboratory worker, *Lab animal*, vol.16, no.6, pp.29-33.

Weigelt, J. (1927) Über Biostratonomie, *Der Geologe*, vol.42, pp.1069-1076.

Weigelt, J. (1989 [1927]) *Recent Vertebrate Carcasses and Their Paleobiological Implications*. University of Chicago Press: Chicago, Illinois.

Wellnhofer, P. (1991) *The Illustrated Encyclopedia of Pterosaurs*. Salamander: London.

West, D.L. and Martin, L.D. (2002) Insect trace fossils as environmental/taphonomic indicators in archaeology and paleoecology, *TER-QUA Symposium Series-Institute for Tertiary-Quaternary Studies*, vol.3, pp.163-173.

White, E.I. (1946) The genus *Phialaspis* and the "Psammosteus limestones", *Journal of Geological Society, London*, vol.101, pp.207-242.

White, T. (1986) Cut marks on the Bodo cranium: a case of prehistoric defleshing, *American Journal of Physical Anthropology*, vol.69, pp.503-509.

White, T. (1992) *Prehistoric Cannibalism at Mancos 5MTUMR-2346*. Princeton University Press: Princeton, New Jersey.

White, T. and Toth, N. (1989) Engis: preparation damage, not ancient cutmarks, *American Journal of Physical Anthropology*, vol.78, pp.361-367.

White, T.D., Suwa, G. and Asfaw, B. (1994) *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethopia, *Nature*, vol.371, pp.306-312.

White, T.D., Asfaw, B., Beyene, Y., Haile-Selassie, Y., Lovejoy, C.O., Suwa, G. and WoldeGabriel, G. (2009a) *Ardipithecus ramidus* and the paleobiology of early hominids, *Science*, vol.326, pp.75-86.

White, T.D., Ambrose, S.H., Suwa, G., Su, D.F., DeGusta, D., Bernor, R.L., Boisserie, J.-R., Brunet, M., Delson, E., Frost, S., Garcia, N., Giaourtsakis, I.X., Haile-Selassie, Y., Howell, F.C., Lehmann, T., Likius, A., Pehlevan, C., Saegusa, H., Semprebon, G., Teaford, M and Vrba, E.S. (2009b) Macrovertebrate paleontology and the Pliocene habitat of *Ardipithecus ramidus*, *Science*, vol.326, pp.87-93.

Whybrow, P.J. (1985) A history of fossil collecting and preparation techniques, *Curator: The Museum Journal*, vol.28, no.1, pp.5-26.

Wilkinson, M.J. (1983) Geomorphic perspectives on the Sterkfontein Australopithecine breccias, *Journal of Archaeological Science*, vol.10, pp.515-529.

Willey, P. and Heilmann, A. (1987) Estimating time since death using plant roots and stems, *Journal of Forensic Sciences*, vol.32, pp.1264-1270.

Wilson, D.E. (1975) Factors Affecting Roan and Sable Antelope Populations on Nature Reserves in the Transvaal with Particular Reference to Ecophysiological Aspects, D.Sc. thesis, University of Pretoria.

Wilson, M.V.H. (1988) Taphonomic processes: information loss and information gain, *Geoscience Canada*, vol.15, no.2, pp.131-148.

Wind, J (1984) Computerized X-ray tomography of fossil hominid skulls, *American Journal of Physical Anthropology*, vol.63, pp.265–282.

Wood, W.R. and Johnson, D.L. (1978) A survey of disturbance processes in archaeological site formation, In: Schiffer, M.B. (ed.) *Advances in archaeological method and theory*, pp. 315-381. New York: Academic Press.

Wrangham, R.W. (1999) Evolution of coalitionary killing, *Yearbook of Physical Anthropology*, vol.42, pp.1-30.

Wrangham, R.W. and Peterson, D. (1996) *Demonic Males*. Houghton Mifflin: New York.

Wu, X. and Schepartz, L.A. (2009) Application of computed tomography in paleoanthropological research, *Progress in Natural Science*, vol.19, pp.913-921.

Wynn, J.G., Alemseged, Z., Bobe, R., Geraads, D., Reed, D. and Roman, D. (2006) Geological and palaeontological context of a Pliocene juvenile hominin at Dikika, Ethiopia, *Nature*, vol.443, pp.332-336.

Zeigler, K.E., Heckert, A.B., and Lucas, S.G. (2002) A tale of two sites: a taphonomic comparison of two late Triassic (Chinle Group) vertebrate fossil localities from New Mexico, *New Mexico Museum of Natural History and Science Bulletin*, no.21, pp.285-290.

Zihlman, A.L., Bolter, D.R. and Boesch, C. (2007) Skeletal and dental growth and development in chimpanzees of the Taï National Park, Côte d'Ivoire, *Journal of Zoology*, vol.273, pp.63-73.

Zipfel, B. and Berger, L.R. (2009) New Cenozoic fossil-bearing site abbreviations for collections of the University of the Witwatersrand, *Palaeontologica Africana*, vol.44, pp.77-81.

Zipfel, B., DeSilva, J.M., Kidd, R.S, Carlson, K.J., Churchill, S.E. and Berger, L.R. (2011) The foot and ankle of *Australopithecus sediba*, *Science*, vol.333, pp.1417-1420.

Zollikofer, C.P.E., Ponce de León, M.S. and Martin, R.D. (1998) Computer-assisted paleoanthropology, *Evolutionary Anthropology*, vol.6, pp.41-54.

Zollikofer, C.P.E., Ponce de León, M.S., Vandermeersch, B. and Lévêque, F. (2002) Evidence for interpersonal violence in the St. Césaire Neanderthal, *PNAS*, vol.99, no.9, pp.6444-6448.

Zollikofer, C.P.E., Ponce de León, M.S., Lieberman, D.E., Guy, F., Pilbeam, D., Likius, A., Mackaye, H.T., Vignaud, P. and Brunet, M. (2005) Virtual cranial reconstruction of *Sahelanthropus tchadensis*, *Nature*, vol.434, pp.755-759.

Zollikofer, C.P.E. and Ponce de León, M.S. (2005) *Virtual Reconstruction. A Primer in Computer-Assisted Paleontology and Biomedicine*. John Wiley & Sons, INC., publication.

**Appendix 1.** Hominin specimens, with a description of their anatomy and provenance in the deposit.

| **Specimen** | **Element** | **Individual** | **Origin** | ***Ex situ*/*In situ*** |
|---|---|---|---|---|
| UW88-31 | Fragment of the right parietal | MH1 | Decalcified sediment, Facies D | *In situ* |
| UW88-32 | Fragment of the right temporal | MH1 | | |
| UW88-16 | Right metatarsal | MH1? | Decalcified sediment, West of Facies D | *In situ* |
| UW88-22 | Right metatarsal | MH1? | | |
| UW88-29 | Upper first right incisor | MH1 | Decalcified sediment (sieving), Facies D | *In situ* |
| UW88-30 | Upper right canine | MH1 | | |
| UW88-1 | Right clavicle shaft | MH1 | Clavicle block | *Ex situ* |
| UW88-2 | Right mandible with canine | MH1 | | |
| UW88-3 | Proximal right ulna | MH1 | | |
| UW88-6 | Anterior fragment of the right ilium | MH1 | | |
| UW88-7 | Posterior fragment of the right ilium | MH1 | | |
| UW88-8 | Right hemi-mandible | MH1 | | |
| UW88-14 | Left ischium | MH1 | | |
| UW88-9 | Cervical vertebra | MH1 | | |
| UW88-11 | Thoracic vertebra | MH1 | | |
| UW88-12 | Distal epiphysis of the right radius | MH1 | | |
| UW88-13 | Distal fragment of a right rib | MH1 | | |
| UW88-17 | Rib fragment | MH1 | | |

| | | | | |
|---|---|---|---|---|
| UW88-113 | Fragmentary right acromion process | MH1 | | |
| UW88-4 | Proximal right femur | MH1 | miner's dump | *Ex situ* |
| UW88-5 | Proximal right femur | MH1 | | |
| UW88-39 | Proximal right femur | MH1 | | |
| UW88-89 | Right femoral shaft | MH1 | | |
| UW88-42 | Right humeral shaft | MH1 | Skull block | *Ex situ* |
| UW88-35 | Left humeral head | MH1 | | |
| UW88-50 | Skull | MH1 | | |
| UW88-88 | Distal right humerus | MH1 | Ilium block | *Ex situ* |
| UW88-102 | Left ilium | MH1 | | |
| no number | Left femur | MH1 | UW88-B051 | *Ex situ* |
| no number | Left clavicle | MH1 | | |
| no number | Fibula | MH1 | | |
| no number | Left hemi-mandible | MH1 | | |
| no number | Distal right ulna | MH1 | | |
| no number | Intermediate rib | MH1 | | |
| no number | Intermediate rib | MH1 | | |
| no number | Intermediate rib | MH1 | | |
| no number | Possible humeral shaft | MH1 | | |
| no number | Radius/Rib | MH1 | | |

| | | | | |
|---|---|---|---|---|
| no number | Possible distal humerus | MH1 | | |
| no number | Tibia/distal femur | MH1 | | |
| no number | Hand/foot bone | MH1 | | |
| no number | Hand/foot bone | MH1 | | |
| no number | Hand/foot bone | MH1 | | |
| no number | Hand/foot bone | MH1 | | |
| no number | Hand/foot bone | MH1 | | |
| UW88-152 | First lumbar vertebra | MH1 | UW88-B245 | *Ex situ* |
| UW88-155 | Intermediate rib | MH1 | | |
| UW88-41 | Intermediate right rib | MH1 | miner's dump | *Ex situ* |
| UW88-86 | Proximal right rib | MH1 | | |
| UW88-67 | Ilium fragment | MH1 | miner's dump | *Ex situ* |
| UW88-206 | Ilium fragment | MH1 | miner's dump | *Ex situ* |
| UW88-27 | Pelvic fragment | MH1 | miner's dump | *Ex situ* |
| UW88-35 | Possible scapula fragment | MH1 | miner's dump | *Ex situ* |
| UW88-68 | Scapula fragment | MH1 | miner's dump | *Ex situ* |
| UW88-197 | Left scapula fragment | MH1 | UW88-B057 | *Ex situ* |
| UW88-112 | Right metacarpal | MH1 | miner's dump | *Ex situ* |
| UW88-34 | Right humeral head | MH1 | miner's dump | *Ex situ* |
| UW88-130 | Distal left ulna | MH1 | miner's dump | *Ex situ* |

| | | | | |
|---|---|---|---|---|
| UW88-18 | Radius fragment | MH1 | miner's dump | *Ex situ* |
| UW88-75 | Radius fragment | MH1 | miner's dump | *Ex situ* |
| UW88-26 | Long bone fragment | MH1 | miner's dump | *Ex situ* |
| UW88-77 | Long bone fragment | MH1 | miner's dump | *Ex situ* |
| UW88-148 | First right rib | MH1 | miner's dump | *Ex situ* |
| UW88-74 | Distal rib fragment | MH1 | miner's dump | *Ex situ* |
| UW88-211 | Intermediate rib fragment | MH1 | miner's dump | *Ex situ* |
| UW88-141 | Possible right rib fragment | MH1 | miner's dump | *Ex situ* |
| UW88-76 | Sternal end of a rib | MH1 | miner's dump | *Ex situ* |
| UW88-71 | Fragmentary cervical vertebra | MH1 | miner's dump | *Ex situ* |
| UW88-92 | Lumbar vertebra | MH1 | miner's dump | *Ex situ* |
| UW88-37 | Thoracic vertebra | MH1 | miner's dump | *Ex situ* |
| UW88-69 | Thoracic vertebra | MH1 | miner's dump | *Ex situ* |
| UW88-70 | Thoracic vertebra | MH1 | miner's dump | *Ex situ* |
| UW88-90 | Thoracic vertebra | MH1 | miner's dump | *Ex situ* |
| UW88-72 | Cervical vertebra | MH1 | miner's dump | *Ex situ* |
| UW88-93 | Cervical vertebra | MH1 | miner's dump | *Ex situ* |
| UW88-73 | Vertebra | MH1 | miner's dump | *Ex situ* |
| UW88-28 | Scapula | MH2 | Arm block (UW88-B043) | *In situ* |
| UW88-57 | Right humerus | MH2 | Facies D | |

| | | | | |
|---|---|---|---|---|
| UW88-62 | Right ulna | MH2 | | |
| UW88-85 | Right radius | MH2 | | |
| UW88-172 | Manubrium | MH2 | | |
| UW88-63 | Distal right femur | MH2 | | |
| UW88-198 | First right rib | MH2 | | |
| UW88-58 | Second right rib | MH2 | | |
| UW88-61 | Intermediate right rib | MH2 | | |
| UW88-154 | Intermediate rib | MH2 | | |
| UW88-59 | Rib fragment | MH2 | | |
| UW88-60 | Rib fragment | MH2 | | |
| UW88-143 | Right rib fragment | MH2 | | |
| UW88-144 | Right rib fragment | MH2 | | |
| UW88-145 | Right rib fragment | MH2 | | |
| UW88-165 | Right rib fragment | MH2 | | |
| UW88-119 | First right metacarpal | MH2 | | |
| UW88-115 | Second right metacarpal | MH2 | | |
| UW88-116 | Third right metacarpal | MH2 | | |
| UW88-117 | Fourth right metacarpal | MH2 | | |
| UW88-118 | Fifth right metacarpal | MH2 | | |
| UW88-95 | Right hamate | MH2 | | |

| | | | | |
|---|---|---|---|---|
| UW88-156 | Right capitate | MH2 | | |
| UW88-158 | Right scaphoid | MH2 | | |
| UW88-159 | Right lunate | MH2 | | |
| UW88-163 | Right triquetral | MH2 | | |
| UW88-160 | First proximal right phalanx | MH2 | | |
| UW88-164 | Second proximal right phalanx | MH2 | | |
| UW88-120 | Third proximal right phalanx | MH2 | | |
| UW88-108 | Fourth proximal right phalanx | MH2 | | |
| UW88-121 | Fifth proximal right phalanx | MH2 | | |
| UW88-123 | Second intermediate right phalanx | MH2 | | |
| UW88-161 | Third intermediate right phalanx | MH2 | | |
| UW88-122 | Fourth intermediate right phalanx | MH2 | | |
| UW88-162 | Fifth intermediate right phalanx | MH2 | | |
| UW88-124 | First distal right phalanx | MH2 | | |
| UW88-79 | Right patella | MH2 | Knee articulated, top of the arm block<br>(UW88-B043)<br>Facies D | *In situ* |
| UW88-100 | Right patella | MH2 | | |
| UW88-64 | Proximal right tibia | MH2 | | |
| UW88-78 | Proximal right tibia | MH2 | | |
| UW88-56 | Cranial fragment of the right scapula | MH2 | Scapula fragment block | *Ex situ* |
| UW88-54 | Right hemi-mandible (fragment) | MH2 | | |

| | | | | |
|---|---|---|---|---|
| UW88-19 | Second upper left molar | MH2 | | |
| UW88-20 | Third upper left molar | MH2 | | |
| UW88-38 | Right clavicle | MH2 | | |
| UW88-83 | Cervical vertebra | MH2 | | |
| UW88-133 | Right pelvis | MH2 | Pelvis block (UW88-B079) | *Ex situ* |
| UW88-134 | Left pelvis (fragment) | MH2 | | |
| UW88-135 | Left pelvis (fragment) | MH2 | | |
| UW88-137 | Sacrum | MH2 | | |
| UW88-138 | Last lumbar (fragment) | MH2 | | |
| UW88-153 | Last lumbar (fragment) | MH2 | | |
| UW88-97 | Distal right tibia | MH2 | Ankle | *Ex situ* |
| UW88-99 | Right calcaneum | MH2 | | |
| UW88-98 | Right talus | MH2 | | |
| UW88-43 | Thoracic vertebra | MH2 | Thoracic vertebrae block 1 | *Ex situ* |
| UW88-44 | Thoracic vertebra | MH2 | | |
| UW88-45 | Rib | MH2 | | |
| UW88-46 | Rib | MH2 | | |
| UW88-47 | Rib | MH2 | | |
| UW88-48 | Rib | MH2 | | |
| UW88-114 | Fragmentary thoracic vertebra | MH2 | | |

| | | | | |
|---|---|---|---|---|
| UW88-177 | Possible metatarsal fragment | MH2? | Thoracic vertebrae block 2<br><br>(UW88-B742) | *Ex situ* |
| UW88-178 | Second proximal left rib | MH2 | | |
| UW88-179 | Pedal distal phalanx | MH2 | | |
| UW88-180 | Sesamoid | MH2 | | |
| UW88-181 | Proximal part of the first metatarsal | MH2 | | |
| UW88-183 | Unidentifiable bone fragment | MH2 | | |
| UW88-185 | Unidentifiable bone fragment | MH2 | | |
| UW88-187 | Proximal part of the first left rib | MH2 | | |
| UW88-188 | Thoracic vertebra | MH2 | | |
| UW88-189 | Thoracic vertebra | MH2 | | |
| UW88-190 | Thoracic vertebra | MH2 | | |
| UW88-191 | Thoracic vertebra | MH2 | | |
| UW88-125 | Fragment of the sacrum | MH2 | Lumbar vertebra block | *Ex situ* |
| UW88-126 | Lumbar vertebra | MH2 | | |
| UW88-127 | Lumbar vertebra | MH2 | | |
| UW88-55 | Left mandible with third molar | MH2 | miner's dump | *Ex situ* |
| UW88-55b | Fragment of the left mandible | MH2 | | |
| UW88-23 | Proximal left fibula | MH2 | miner's dump | *Ex situ* |
| UW88-84 | Proximal left fibula | MH2 | | |
| UW88-146 | Fragmentary right fibula shaft | MH2 | miner's dump | *Ex situ* |

| | | | | |
|---|---|---|---|---|
| UW88-202 | Fragmentary right fibula shaft | MH2? | West of Facies D | *Ex situ* |
| UW88-103 | Left acromion (scapula) | MH2 | miner's dump | *Ex situ* |
| UW88-104 | Left scapula fragment (glenoid) | MH2 | miner's dump | *Ex situ* |
| UW88-101 | Left humeral head | MH2 | miner's dump | *Ex situ* |
| UW88-87 | Distal left femur | MH2 | miner's dump | *Ex situ* |
| UW88-94 | Lateral end of the left clavicle | MH2 | miner's dump | *Ex situ* |
| UW88-10 | Left pubis (fragment) | MH2 | miner's dump | *Ex situ* |
| UW88-136 | Right pelvis (fragment) | MH2 | miner's dump | *Ex situ* |
| UW88-65 | Distal right fibula | MH2 | miner's dump | *Ex situ* |
| UW88-24 | Proximal left tibia | MH2 | miner's dump | *Ex situ* |
| UW88-192 | Rib fragment | MH2 | UW88-B1003 | *Ex situ* |
| UW88-193 | Rib fragment | MH2 | | |
| UW88-209 | Rib fragment | MH2 | miner's dump | *Ex situ* |
| UW88-210 | Rib fragment | MH2 | miner's dump | *Ex situ* |
| UW88-96 | Fragmentary cervical vertebra | MH2 | miner's dump | *Ex situ* |
| UW88-182 | Proximal left metacarpal | MH2 | UW88-B894 | *Ex situ* |
| UW88-157 | Unidentifiable hand bone | MH2 | miner's dump | *Ex situ* |
| UW88-91 | Proximal part of the pedal left phalanx | MH2 | miner's dump | *Ex situ* |
| UW88-150 | Left capitate | MH2 | miner's dump | *Ex situ* |
| UW88-106 | Left hamate | MH2 | miner's dump | *Ex situ* |

| | | | | |
|---|---|---|---|---|
| UW88-107 | Left triquetral | MH2 | miner's dump | *Ex situ* |
| UW88-201 | Molar crown fragment | MH2 | miner's dump | *Ex situ* |
| UW88-175 | Proximal right femur | MH3 | miner's dump | *Ex situ* |
| UW88-176 | Unidentified bone fragment | MH3 | | |
| UW88-21 | Distal right tibia | MH4 | miner's dump | *Ex situ* |
| UW88-40 | Proximal right tibia | MH4 | | |
| UW88-81 | Distal right humerus | MH5 | Facies E | *In situ* |
| UW88-82 | Proximal right ulna | MH5 | | |
| No number | Mandible with teeth | MH6 | Facies F, Pit 2 | *In situ* |
| UW88-33 | Fifth proximal metatarsal | MH? | miner's dump | *Ex situ* |
| UW88-149 | Distal radius | MH? | miner's dump | *Ex situ* |
| UW88-150 | Distal fibula | MH? | miner's dump | *Ex situ* |
| UW88-151 | Femoral head fragment | MH? | miner's dump | *Ex situ* |
| UW88-169 | Fragmentary mandible | MH? | Facies F, Pit 2 | *In situ* |
| UW88-208 | Fragment ulna shaft | MH? | Facies D | *In situ* |
| UW88-219 | Fragment ulna shaft | MH? | | |
| UW88-186 | Mandible fragment | MH? | miner's dump | *Ex situ* |
| UW88-213 | Intermediate phalanx | MH? | miner's dump | *Ex situ* |
| UW88-218 | Unfused epiphysis | MH? | miner's dump | *Ex situ* |
| UW88-194 | Possible pelvic fragment | MH? | miner's dump | *Ex situ* |

| | | | | |
|---|---|---|---|---|
| UW88-195 | Possible pelvic fragment | MH? | | |
| UW88-199 | Rib fragment | MH? | miner's dump | *Ex situ* |
| UW88-205 | Rib fragment | MH? | miner's dump | *Ex situ* |
| UW88-140 | Ulna shaft fragment | MH? | miner's dump | *Ex situ* |
| UW88-204 | Fibula shaft fragment | MH? | miner's dump | *Ex situ* |
| UW88-207 | Fibula shaft fragment | MH? | miner's dump | *Ex situ* |
| UW88-217 | Fibula shaft fragment | MH? | miner's dump | *Ex situ* |
| UW88-220 | Fibula shaft fragment | MH? | miner's dump | *Ex situ* |
| UW88-212 | Rib fragment | MH? | miner's dump | *Ex situ* |
| UW88-214 | Rib fragment | MH? | miner's dump | *Ex situ* |
| UW88-215 | Rib fragment | MH? | miner's dump | *Ex situ* |
| UW88-216 | Right clavicle fragment | MH? | miner's dump | *Ex situ* |
| UW88-139 | cuneiform | MH? | miner's dump | *Ex situ* |

**Appendix 2.** Coordinates of the *in situ* hominin remains.

| Specimen number | Element | Individual | Coordinates | | |
|---|---|---|---|---|---|
| | | | *E (x)* | *N (y)* | *Depth (z)* |
| UW88-31 | Vault fragment (right parietal) | MH1 | -80313.00 | 2865448.24 | 1442.95 |
| UW88-32 | Vault fragment (right temporal) | MH1 | -80313.00 | 2865448.24 | 1442.95 |
| UW88-29 | Upper right incisor | MH1 | -80313.20 | 2865448.44 | 1443.00 |
| UW88-30 | Upper right canine | MH1 | -80313.20 | 2865448.44 | 1443.00 |
| UW88-16 | Right metatarsal | MH1? | -80311.71 | 2865448.74 | 1441.69 |
| UW88-22 | Right metatarsal | MH1? | -80311.71 | 2865448.74 | 1441.69 |
| UW88-B043 | Arm block-north corner | MH2 | -80312.90 | 2865448.69 | 1442.49 |
| UW88-B043 | Arm block-south corner | MH2 | -80313.15 | 2865449.20 | 1442.19 |
| UW88-B043 | Arm block-west corner | MH2 | -80312.84 | 2865449.01 | 1442.30 |
| UW88-B043 | Arm block-east corner | MH2 | -80311.71 | 2865449.00 | 1442.51 |
| UW88-B043 | Arm block-centre | MH2 | -80312.43 | 2865448.94 | 1442.35 |
| UW88-202 | Fibula shaft fragment | MH2? | -80316.51 | 2865448.50 | 1444.06 |
| UW88-175 | Proximal right femur | MH3 | ND | ND | ND |
| UW88-176 | Unidentified bone fragment | MH3 | ND | ND | ND |
| UW88-81 | Distal right humerus | MH3 | ND | ND | ND |
| UW88-82 | Proximal right ulna | MH3 | ND | ND | ND |
| UW88-169 | Mandible | MH5 | -80310.79 | 2865441.95 | 1443.69 |

| | | | | | |
|---|---|---|---|---|---|
| No number | Mandible with teeth | MH6 | ND | ND | ND |
| UW88-208 | Ulna shaft fragment | MH? | -80316.95 | 2865448.30 | 1444.02 |
| UW88-219 | Ulna shaft fragment | MH? | -80315.11 | 2865444.98 | 1443.81 |

ND: not documented

**Appendix 3.** Thesaurus for the faunal database.

**List of abbreviations used throughout the database**

- CO: complete
- NA: not applicable
- ND: non documented
- fgmt: fragment

**List of abbreviations used for the taxonomy**

- ARTIO: artiodactyla
- AVES: bird
- BOV: bovid
- CARN: carnivore
- CHEL: chelonia
- LAGO: lagomorpha
- MAM: mammal
- MIF: microfauna
- PERISSO: perissodactyla
- ROD: rodent
- SMAM: small mammal
- UNG: ungulate

**List of abbreviations used for the anatomy (body part, portion and segment)**

- ACET: acetabulum
- ACRO: acromion
- ALV: alveolar surface
- ANT: anterior
- ART: articular
- ATL: atlas
- AX: axis
- C: canine
- CALC: calcaneum
- CALV: calvarium
- CARP: carpals
- CAPIT: capitate
- CAU: caudal vertebra
- CLAV: clavicle
- CORAC: coracoid
- CRA: cranium (skull+mandible)
- CER: cervical vertebra
- CO: complete
- COX: coxal bone
- CRA: cranium (skull)
- CUBO: cuboid
- CUBO-NAVI: cubo-navicular

- CUN: cuneiform
- D: distal
- DSH: distal part of the shaft
- EP: epiphysis
- FBN: flat bone
- FEM: femur
- FIB: fibula
- fgmt: fragment
- GLEN: glenoid cavity
- HAM: hamate
- HOR: horizontal branch (of the mandible)
- HUM: humerus
- I: incisor
- ILI: ilium
- ISCH: ischium
- LBN: long bones
- LAT: lateral
- LAT MAL: lateral malleolus
- LC: lower canine
- LD: lower deciduous tooth
- LI: lower incisor
- LM: lower molar

- LPM: lower premolar
- LUN: lunate
- LUM: lumbar
- M: molar
- MAG: magnum
- MAN: mandible
- MANT: mandible with teeth
- MANUB: manubrium
- MAX: maxillar
- MAXT: maxillar with teeth
- M: molar
- MDP: manual distal phalanx
- MMP: manual medial (intermediate) phalanx
- MPP: manual proximal phalanx
- META: metapodial
- MTC: metacarpal
- MTT: metatarsal
- OCC: occipital
- P: proximal part
- PAT: patella
- PDP: pedal distal phalanx
- PELV: pelvis

- PHA: phalanx
- PM: premolar
- PMP: pedial medial (intermediate) phalanx
- POST: posterior
- PPP: pedial proximal phalanx
- PROC.: process (for the vertebrae)
- PSH: proximal part of the shaft
- PUB: pubis (coxal bone)
- RAD: radius
- RADIO-ULN: radio-ulna
- RIB: rib
- SAC: sacrum
- SCAP: scapula
- SCAPH: scaphoid
- SES: sesamoid
- SH: shaft
- SHBN: short bone
- SP.PROC.: spinous process (for the vertebrae)
- STERN: sternum/sternal
- SURF: surface
- TAL: talus (astragalus)
- TARS: tarsal

- THO: thoracic vertebra
- TIB: tibia
- TRANS.PROC: transversal process (for the vertebrae)
- TRIQU: triquetral
- TTH: tooth
- UC: upper canine
- UD: upper deciduous tooth
- UI: upper incisor
- ULN: ulna
- UM: upper molar
- UNC: unciform
- UPM: upper premolar
- VER: vertebra
- ZYG: zygomatic

**Fields of the database**

NUMBERING AND PROVENANCE INFORMATION

- **SITE**: Malapa UW-88, consistent with the site number (see Zipfel and Berger, 2009)
- **Number of remains**: usually, each individual specimen is recorded under a separate number; however, in the case of specimens below 2 cm and not analysed for the taphonomy, several fragments are sometimes recorded under the same specimen number. In the case of associated bone (s) and teeth (e.g maxillar or mandible bearing teeth), I have discounted separately the bones and the teeth, in order to take into account each of them as a separate specimen.

- **Suitcase/Box number**: for the hominin remains (each of the MH1 and MH2 remains are kept in different suitcases in the lab) and the non-hominin remains (organised in different boxes in the faunal lab, some of them with a number).
- **Facies**: stratigraphic unit of origin (e.g. Facies D, Facies E) of the *in situ* remains.
- ***Ex situ/In situ***: blocks in place in the place (*in situ*), usually they have been given coordinates (for the block) or blocks that have been removed by the miners (usually found in the road, along the hole).
- **Specimen number**: number given by the people that have identified the faunal remains or from the hominin catalogue (written on the bones themselves). I have created sub-numbers when several remains were recorded under the same number (for example specimen 1142 is composed of 5 bone fragments, which therefore become 1142a, 1142b and so on, always going from the longest fragment to the smallest; hence 1142a is the largest fragment and 1142 e is the smallest).
- **Individual**: name of the individual (only for the hominins: MH1 for the juvenile and MH2 for the adult)
- **Block number:** catalogue number of the block in which the specimen was recovered; it follows the same numbering system UW88-B...
- **Coordinates (east, north and height):** georeferenced coordinates recorded by the theolodite laser, given in metres.
- **Pt:** point recorded in the theodolithe laser, corresponding to the coordinates

<u>IDENTIFICATION (ANATOMY)</u>

- **Nature of the remains**: bone, tooth, horn corn, shell, snail, carapace, stone, coprolite
- **ORDER**: for the faunal remains
- **FAMILY**
- **TRIBE:** only used for the bovids
- **TAXON**: the exact species when identified or the class size, for the mammals, carnivores, bovids and ungulates (following the classification of Brain, 1973).
- **ANAT**: body region to which the bone belongs to (see above for all abbreviations used in that column)
- **BODY PART:** skeleton element (see above for all abbreviations used in that column)

- **PORTION:** portion of the bone that is preserved (e.g. proximal shaft, distal epiphysis, transversal process, etc) (see above for all abbreviations used in that column)
- **SEGMENT:** landmark observed on the fragment allowing the identification (e.g. articular surface, see above for all abbreviations used in that column)
- **AGE**: identified for the hominins and other faunal remains, when possible (e.g. in the case of long bones with epiphysis unfused or deciduous teeth); A: adult, O: old invididual; J: juvenile and I: infant.
- **SEX**: only identified for the hominins (M: male and F: female)
- **FR/CO**: fragmentary (*FR*) or complete (*CO*) (usually not mentioned in the fauna database)
- **SIDE**: right (R), left (*L*) or midline (/)
- **Conjoins with/Joins to**: *with* ... (number of a specimen) when the specimen refits to it or belongs to the same block/individual;*to*...(number of specimen(s)) when it joins two specimens.
- **COMMENTS**: any kind of general comment concerning a specificity of the specimen.

<u>BREAKAGE PATTERN</u>

- **SPONG/COMP**: proportion of spongy and compact bone for each specimen.

*SPONG* : exclusively spongy bone

*COMP*: exclusively compact bone

*SPONG* + *COMP*: spongy and compact bone, with a greater portion of spongy bone

*COMP* + *SPONG*: spongy and compact bone, with a greater portion of compact bone

- **BREAK 1 (PROX):** breakage pattern of the anatomical proximal part of the specimen when identifiable) or, if non identifiable, on one of the end of the longest axis (Figure 1)
- **BREAK 2 (DIST):** breakage pattern of the anatomical distal part of the specimen when identifiable) or, if non identifiable, on the other end of the longest axis (Figure 1)
- **BREAK 3 (LAT)**: breakage pattern of the anatomical lateral part of the specimen when identifiable) or, if non identifiable, on one of the lateral edges (Figure 1)
- **BREAK 4 (MED)**: breakage pattern of the anatomical medial part of the specimen when identifiable) or, if non identifiable, on the other lateral edge (Figure 1)

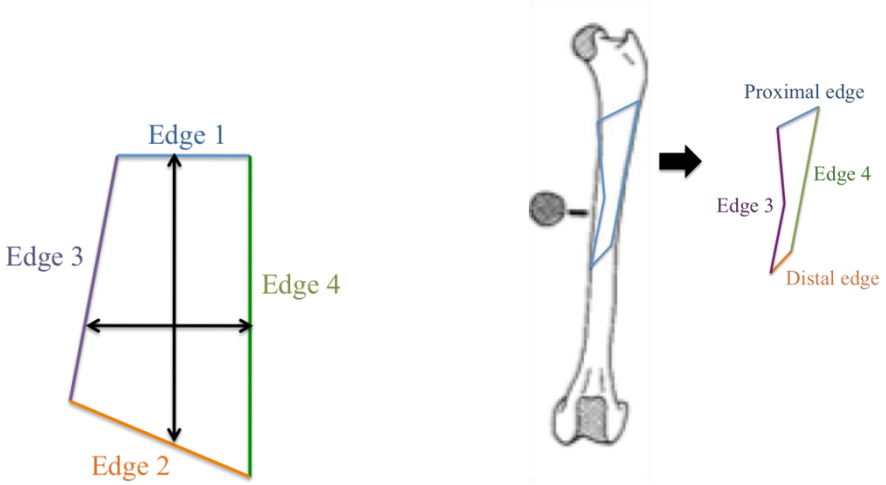



**Figure 1**. Description of the different edges.

DIMENSIONS

All the measurements are given in millimetres.

- **LENGTH**
- **WIDTH**
- **THICK:** thickness
- **CompBoneThick**: thickness of the compact bone
- **CONCH.SCAR:** conchoidal scar (*single*; *multiple isolated*; *multiple adjacent).*

TAPHONOMY

- **WEATHERING**: stages 1 to 5 (cf. Behrensmeyer, 1975)
- **CARN**: carnivore damage (only pits are observed)
- **RODENT**: rodent tooth damage (*large* or *small*)

INVERTEBRATE DAMAGE

- **YES/NO**: presence or absence of any kind of insect modification
- **Inters.Str.**: intersecting striations (YES/NO)
- **Inters.Str. in Pit**: pit with intersecting striations at the bottom (YES/NO)
- **Star-pit**: pit surrounded by parallel striations (YES/NO)
- **Boring** (YES/NO)
- **Paral Str.**: parallel striations (YES/NO)

ABIOTIC DAMAGE

- **ETCHING:** (YES/NO)
- **TRAMPLING:** (YES/NO)
- **ROOTS:** (YES/NO)
- **Calc Crystals:** crystals of calcite formed either on the surface of the bone or inside (in the medullar cavity or in the vessels).
- **Decalcification:** the bone presents a white surface, because the calcium contained in the bone has disappeared (YES/NO)
- **Concretion:** mineral concretion present on the surface of the bone (YES/NO)
- **Abrasion:** any kind of chemical abrasion (due to water for instance but not only).
- **Manganese**: NO (absent), slightly (only a few dots), slightly to moderate (abundant dots), moderate (half the surface of the specimen is covered), moderate to heavily (the majority of the surface is covered with some parts of the surface still visible), and heavily (the whole surface of the specimen is covered)
- **Red traces**: reddish (the colour varies from orangey to dark red) dots and patches observed on the surface of some specimens (YES/NO)

ANTHROPOGENIC MODIFICATIONS

- **BURNING**(natural or anthropogenic origin) Different colour stages (from slightly burned to heavily burned: *maroon, black, grey, white*
- **PREPARATION:** any mark produced by the air drillt used during manual preparation, usually associated with the removal of the specimen from the calcified sediment; it consists of pits and/or scratches
- **POLISH:** the bone or part of it is covered with polish that makes it difficult to see the bone surface
- **PLASTICINE:** presence of specific damage due to the use of plasticine (surface of the bone is dissolved; bits of plasticine are usually still present)
- **PICTURE**: documents whether or not a picture of the specimen exists (either in the Microsoft Access database or in a separate file, also available)
- **COMMENT:** any kind of comment concerning the taphonomy of the specimen

**Appendix 4.** List of antimeric sets of bones present in the Malapa non-hominin faunal assemblage.

| Specimen number | TAXONOMY | BONE | PORTION | SIDE |
|---|---|---|---|---|
| UW88-802 | Felid (cf.*Dinofelis*) | radius | distal | right |
| UW88-803 | Felid (cf.*Dinofelis*) | radius | distal | left |
| UW88-643 | Lagomorph (*Lepus capensis*) | femur | complete | right |
| no number | Lagomorph (*Lepus* sp.) | femur | near complete | left |
| UW88-673 | Lagomorph (*Lepus* sp.) | ilium | complete | left |
| UW88-769 | Lagomorph (*Lepus* sp.) | pelvis | complete | right |
| no number | Lagomorph (*Lepus* sp.) | mandible with teeth | near complete | right |
| no number | Lagomorph (*Lepus* sp.) | mandible with teeth | near complete | left |
| UW88-748 | Bovid class II | femur | complete | right |
| UW88-1181 | Bovid class II | femur | near complete | left |
| UW88-1184 | Bovid class III | humerus | complete | right |
| UW88-1236 | Bovid class III | humerus | proximal | left |
| UW88-507 | Bovid class III | humerus | proximal | right |
| no number | Bovid class III | humerus | proximal | left |
| UW88-1213 | Bovid class III | radius | proximal | right |
| UW88-714 | Bovid class III | radius | proximal | left |
| UW88-1223 | Bovid class II | tibia | complete | right |

| | | | | |
|---|---|---|---|---|
| no number | Bovid class II | tibia | complete | left |
| UW88-1247 | Bovid class III | metacarpal | complete | right |
| UW88-535 | Bovid class III | metacarpal | complete | left |
| UW88-1266 | Bovid class II | scapula blade | near complete | right |
| UW88-1234 | Bovid class II | scapula blade | near complete | left |
| UW88-518 and 519 | Bovid class III (*Tragelaphus* sp.) | mandible with teeth | near complete | right |
| UW88-929 | Bovid class III (*Tragelaphus* sp.) | mandible with teeth | near complete | left |

**Appendix 5.** Quantitative data about the available non-hominin faunal assemblage.

PERCENTAGE OF SURVIVAL FOR BOVID BONES AND TEETH

| Anatomical element | N | NISP | MNE | % survival |
|---|---|---|---|---|
| Skulls | 1 | 16 | 4 | 44.4 |
| Hemi-mandibles | 2 | 10 | 7 | 38.9 |
| Teeth | 32 | 64 | 41 | 14.2 |
| Sternum | 3 | 1 | 1 | 3.7 |
| Ribs | 26 | 34 | 20 | 8.6 |
| Cervical vertebrae | 7 | 8 | 8 | 12.7 |
| Thoracic vertebrae | 13 | 20 | 19 | 16.2 |
| Lumbar vertebrae | 6 | 10 | 7 | 13 |
| Caudal vertebrae | 19 | 5 | 5 | 2.9 |
| **Total vertebrae** | 45 | 32 | 28 | 11.1 |
| Sacrum | 1 | 2 | 2 | 22.2 |
| Coxae | 2 | 11 | 6 | 33.3 |
| Scapulae | 2 | 9 | 5 | 27.8 |
| Humeri | 2 | 8 | 6 | 38.9 |
| Radii | 2 | 10 | 6 | 33.3 |

| | | | | |
|---|---|---|---|---|
| Ulnae | 2 | 5 | 5 | 27.8 |
| Carpals | 12 | 9 | 9 | 8.3 |
| Femurs | 2 | 16 | 9 | 50 |
| Patellae | 2 | 1 | 1 | 5.6 |
| Tibiae | 2 | 7 | 7 | 38.9 |
| Lateral malleolus | 2 | 1 | 1 | 5.6 |
| Tarsals | 10 | 24 | 24 | 26.7 |
| Metapodials | 4 | 25 | 11 | 30.6 |
| Phalanges | 24 | 42 | 33 | 15.3 |
| **TOTAL** | **177** | **322** | **231** | **22.6** |

PERCENTAGE OF SURVIVAL FOR CARNIVORE BONES

| **Anatomical element** | **N** | **NISP** | **MNE** | **% survival** |
|---|---|---|---|---|
| Skulls | 1 | 7 | 5 | 35.7 |
| Hemi-mandibles | 2 | 7 | 5 | 17.9 |
| Ribs | 26 | 11 | 11 | 3.0 |
| Cervical vertebrae | 7 | 2 | 2 | 2.0 |
| Thoracic vertebrae | 13 | 11 | 11 | 6.0 |
| Lumbar vertebrae | 7 | 7 | 7 | 8.3 |

| | | | | |
|---|---|---|---|---|
| Caudal vertebrae | 21 | 2 | 2 | 3.2 |
| **Total vertebrae** | 48 | 21 | 21 | 4.2 |
| Sacrum | 1 | 2 | 2 | 14.3 |
| Scapulae | 2 | 1 | 1 | 3.6 |
| Coxae | 2 | 4 | 4 | 14.3 |
| Humeri | 2 | 2 | 2 | 7.1 |
| Radii | 2 | 5 | 5 | 17.8 |
| Ulnae | 2 | 2 | 2 | 7.1 |
| Carpals | 14 | 5 | 5 | 2.6 |
| Femurs | 2 | 6 | 5 | 17.8 |
| Patellae | 2 | 0 | 0 | 0 |
| Tibiae | 2 | 3 | 3 | 10.7 |
| Fibulae | 2 | 1 | 1 | 3.6 |
| Tarsals | 14 | 10 | 10 | 5.1 |
| Metapodials | 18 | 22 | 21 | 8.3 |
| Phalanges | 52 | 15 | 15 | 2.1 |
| **TOTAL** | **194** | **123** | **118** | **8.9** |

PERCENTAGE OF SURVIVAL FOR CARNIVORE TEETH

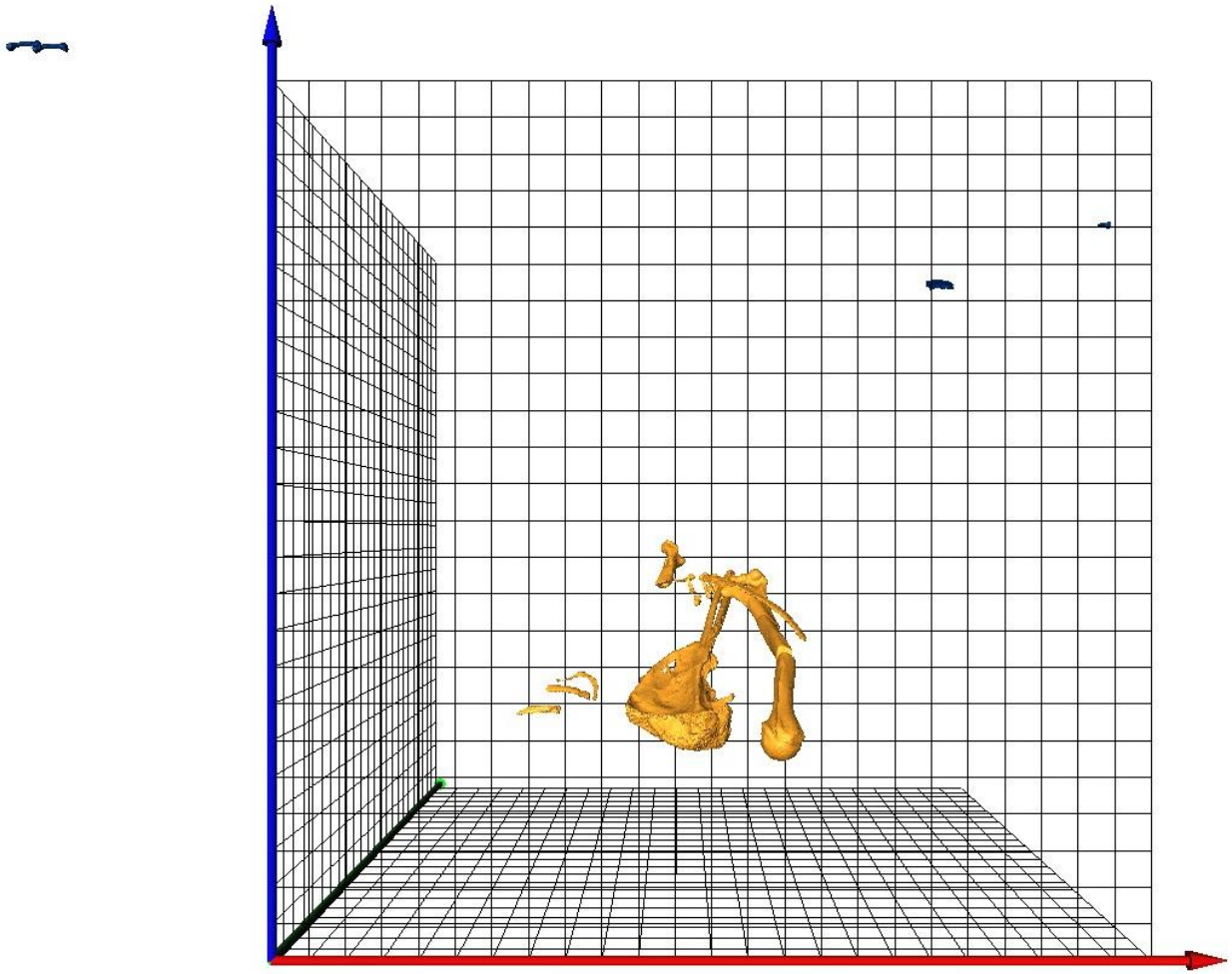
| Unit | Felids | Hyaenids | Canids | Viverrids/Herpestids | TOTAL |
|---|---|---|---|---|---|
| Q | 28 | 34 | 42 | 38 | 142 |
| NISP | 7 | 11 | 5 | 16 | 36 |
| MNE | 7 | 11 | 5 | 16 | 36 |
| % survival | **5** | **10.8** | **6** | **10.5** | **8.2** |

**Appendix 6**. Estimation of the Minimum Number of Individuals (MNI) represented by complete or near complete skeletons.

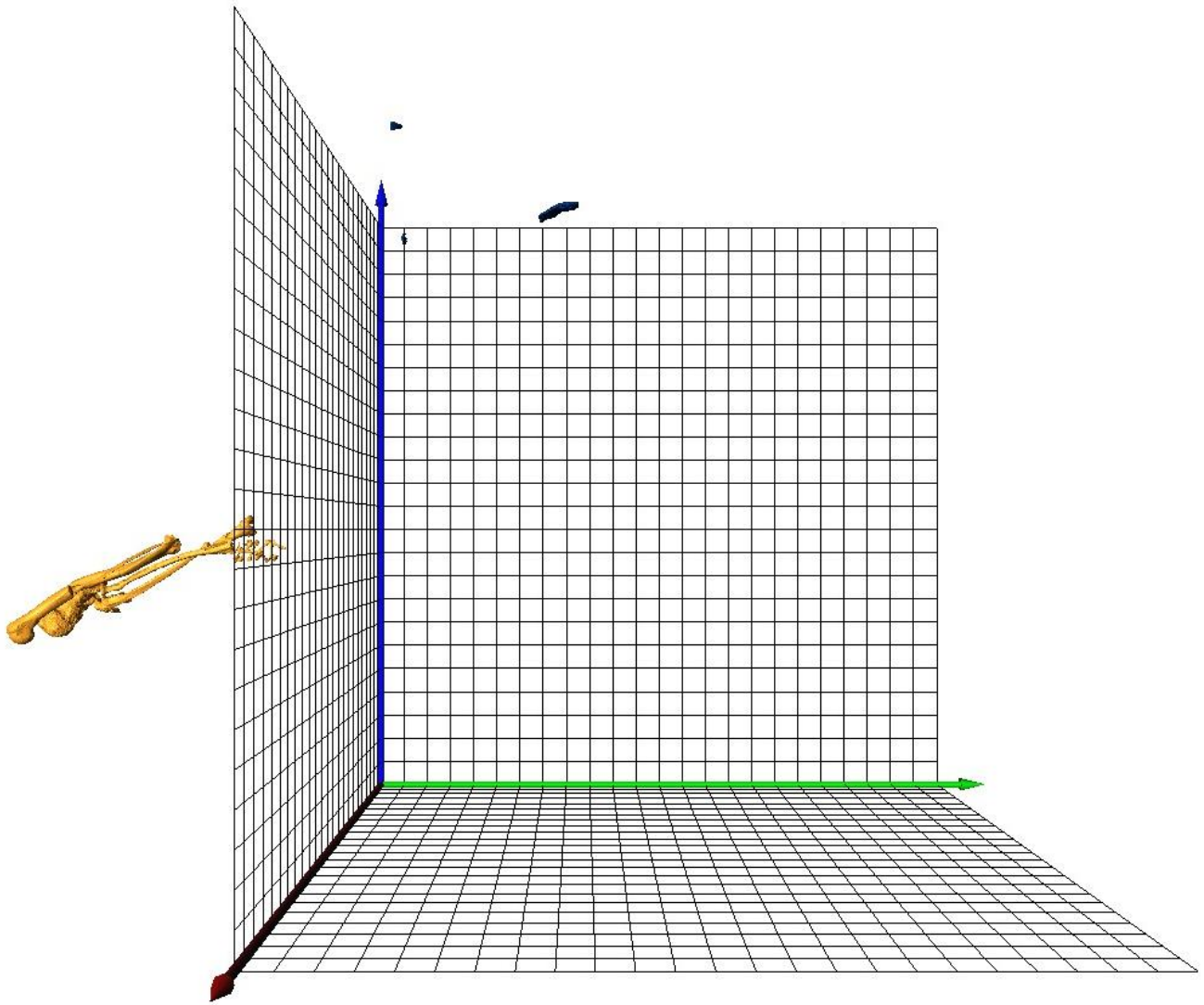
| Species | Individuals/Specimens | MNI |
|---|---|---|
| Hominins | MH1 | 1 |
| | MH2 | 1 |
| Bovid class II | Various elements in articulation, partial skeleton, 3 antimeric sets of bones, one near complete foetus in articulation | 2 |
| Bovid class III (*Tragelaphus* sp.) | Various elements in articulation, partial skeleton, 5 antimeric sets of bones | 1 |
| Small carnivore (possible genet) | Complete upper body-part in articulation and near articulation | 1 |
| Lagomorph (*Lepus* sp.) | Articulated bones, 3 antimeric sets of bones | 1 |
| **TOTAL** | **-** | **7** |

**Appendix 7**. Hypothetical position of the different *ex situ* remains (snapshots from Avizo 6.3).

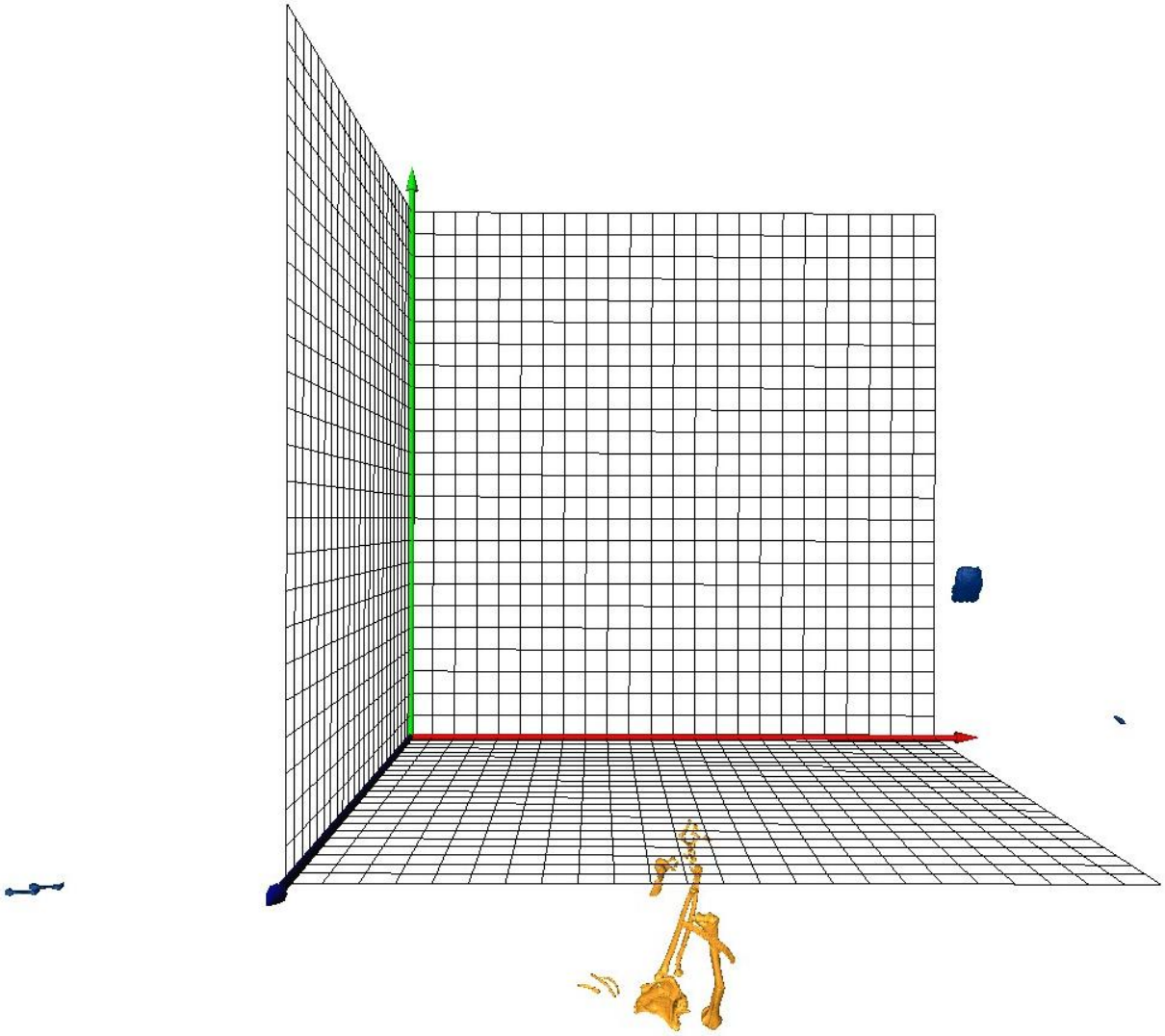
PLACING THE *IN SITU* REMAINS



XZ view (from the south)

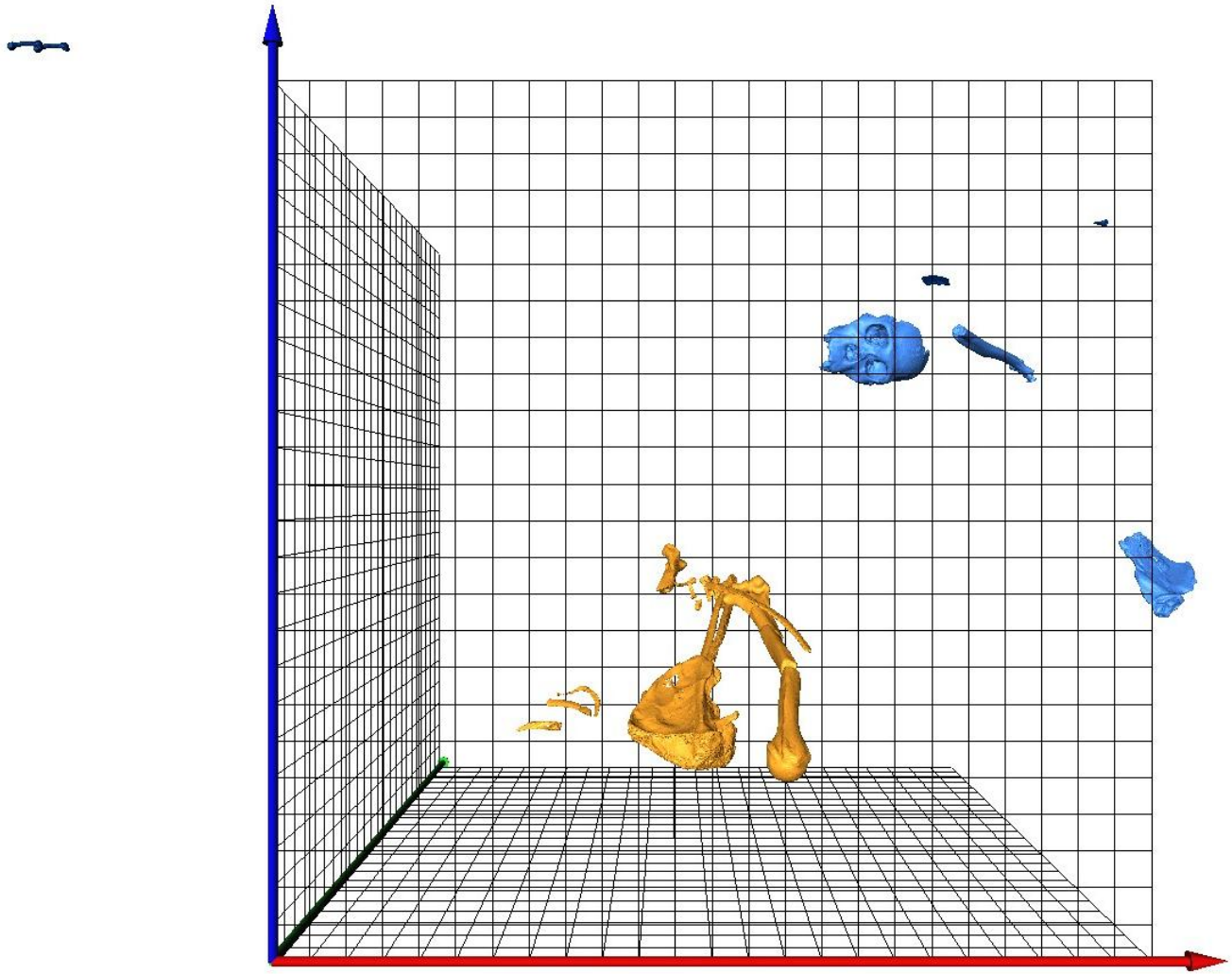


YZ view (from the east)

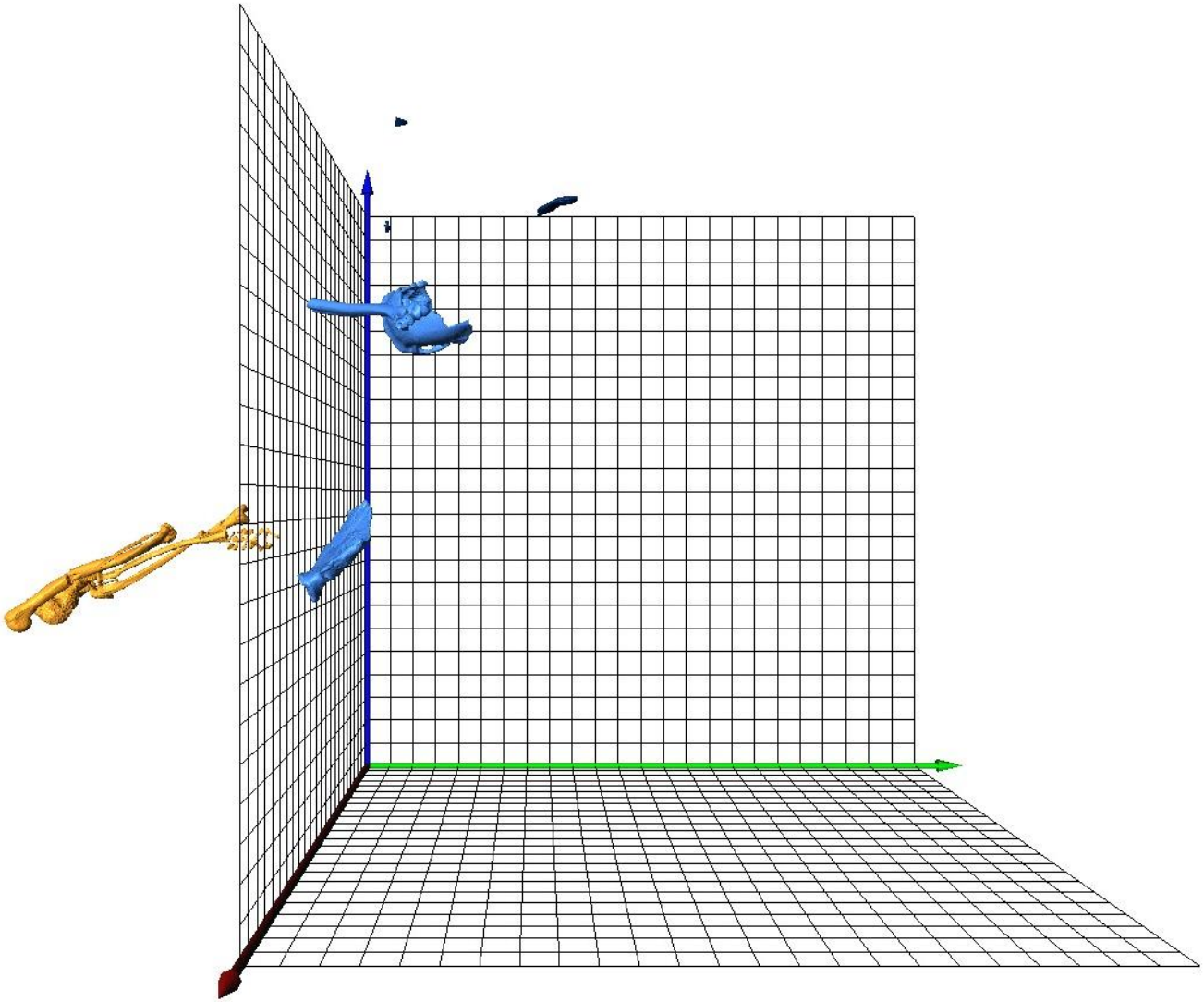


XY view (from the top)

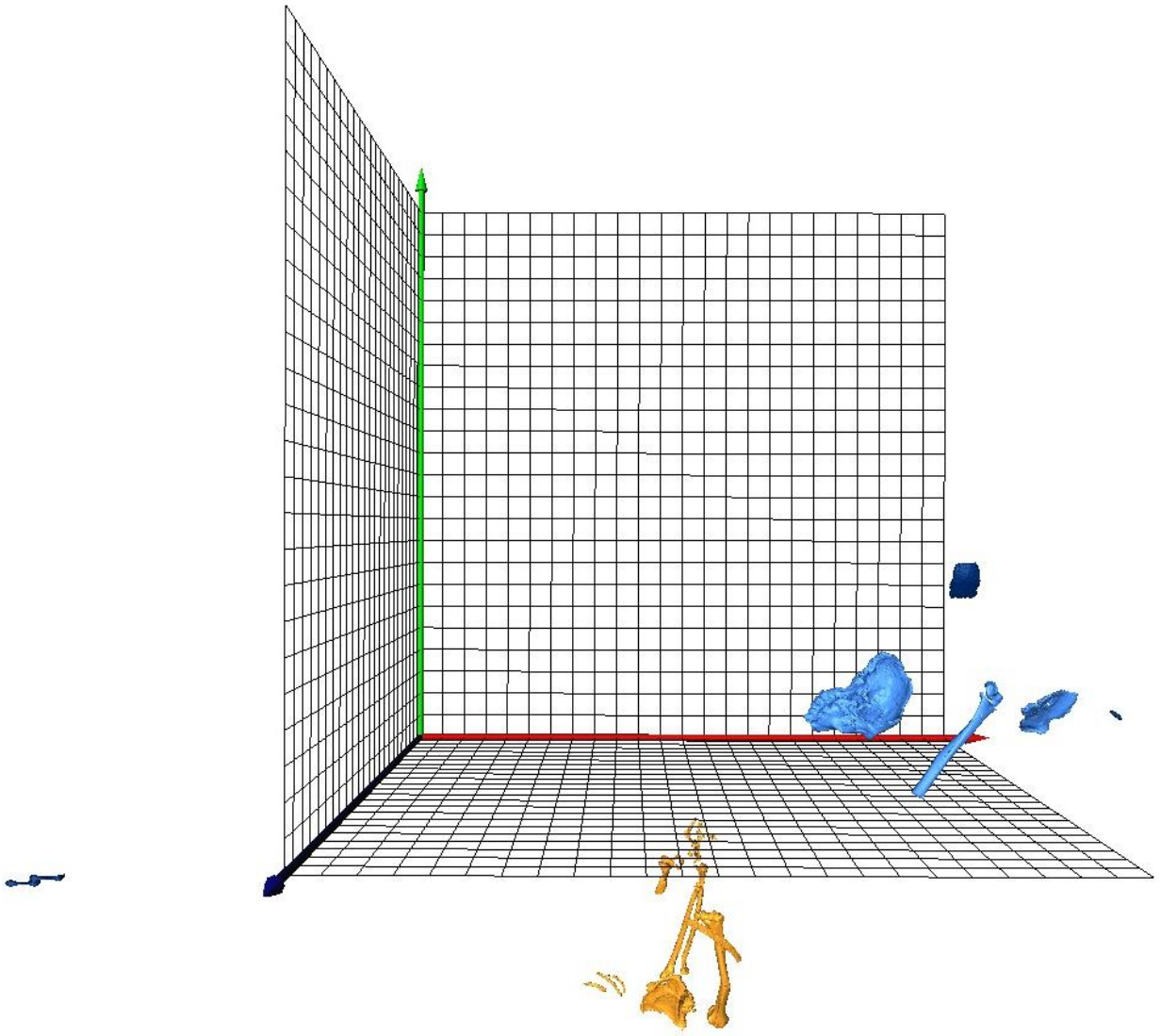
REFITTING MH1 SKULL AND ILIUM BLOCKS



XZ view (from the south)



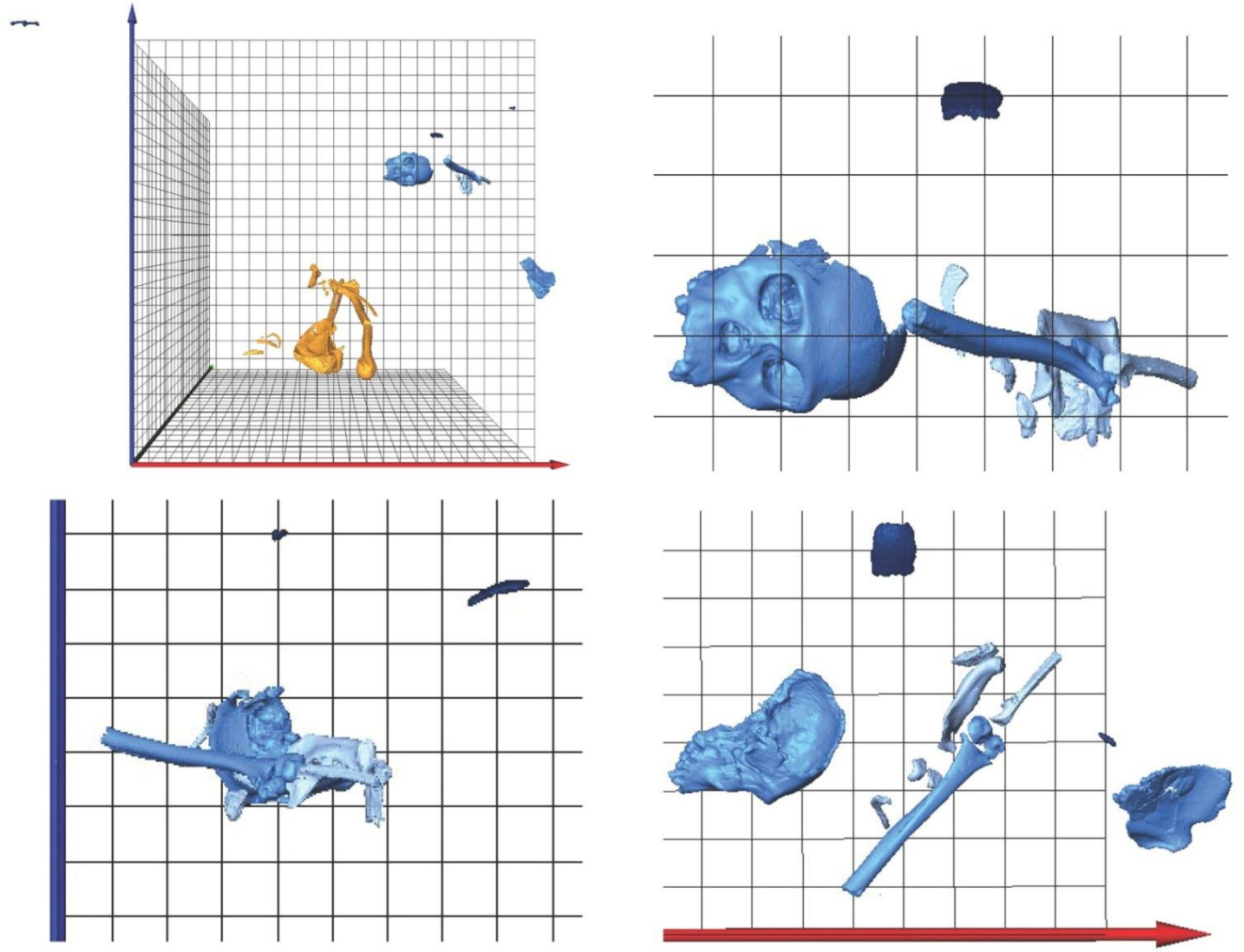
YZ view (from the east)



XY view (from the top)

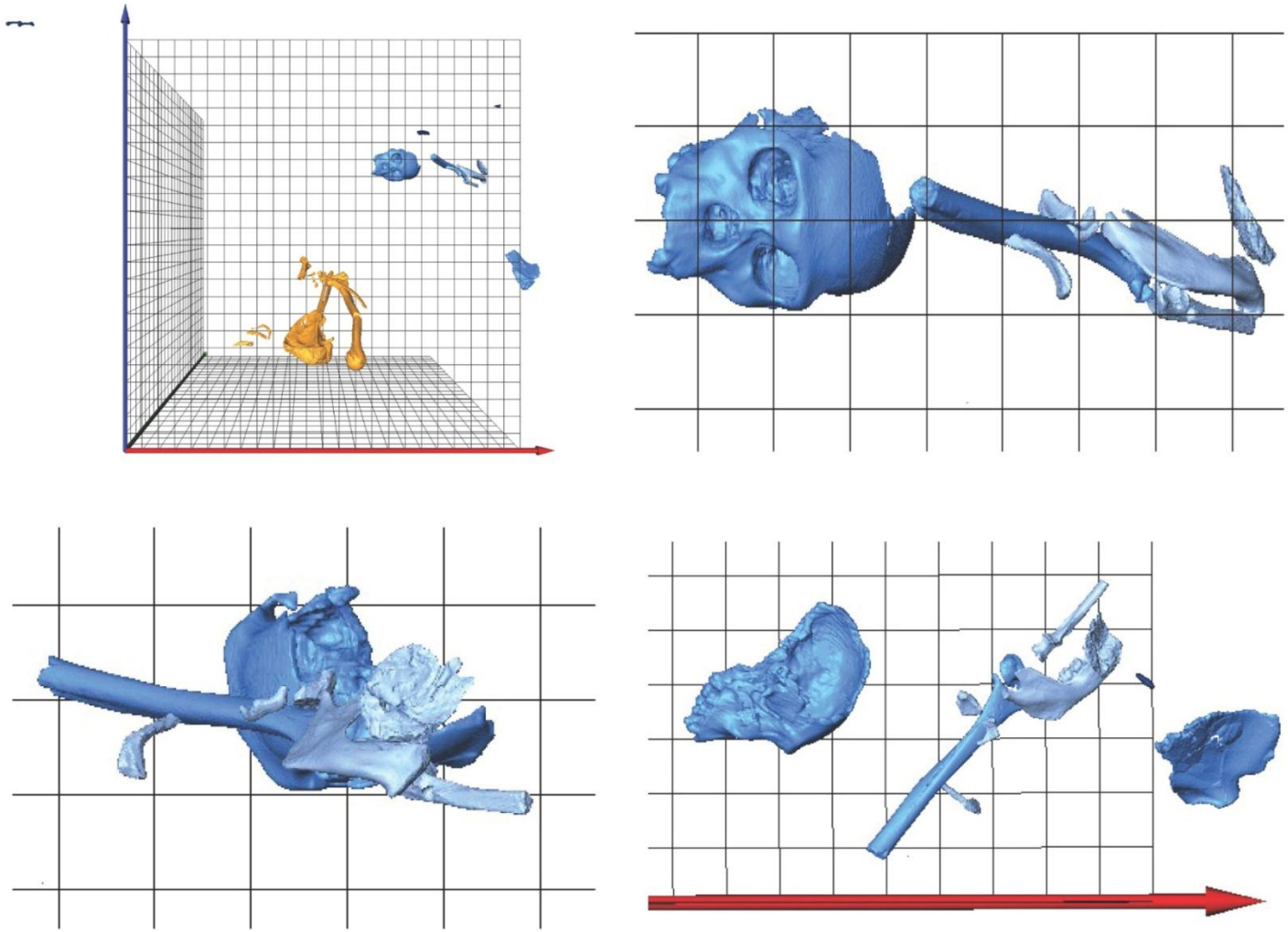
REFITTING MH1 CLAVICLE BLOCK

**Hypothesis 1**



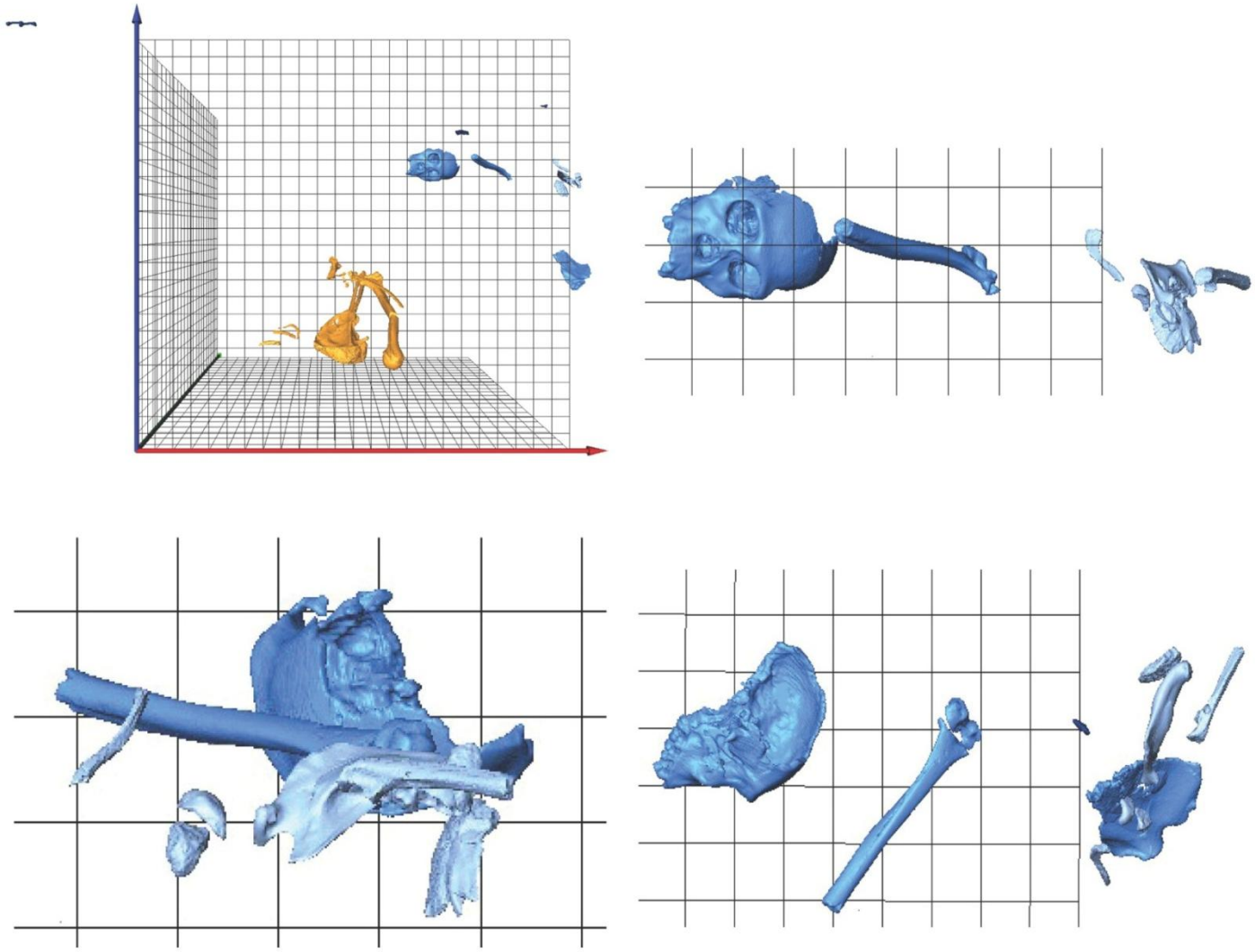
Top left: XZ view (from the south); top right: zoom of the XZ view; bottom left: zoom of the YZ view (from the east); bottom right: zoom of the XY view (from the top)

**Hypothesis 2**



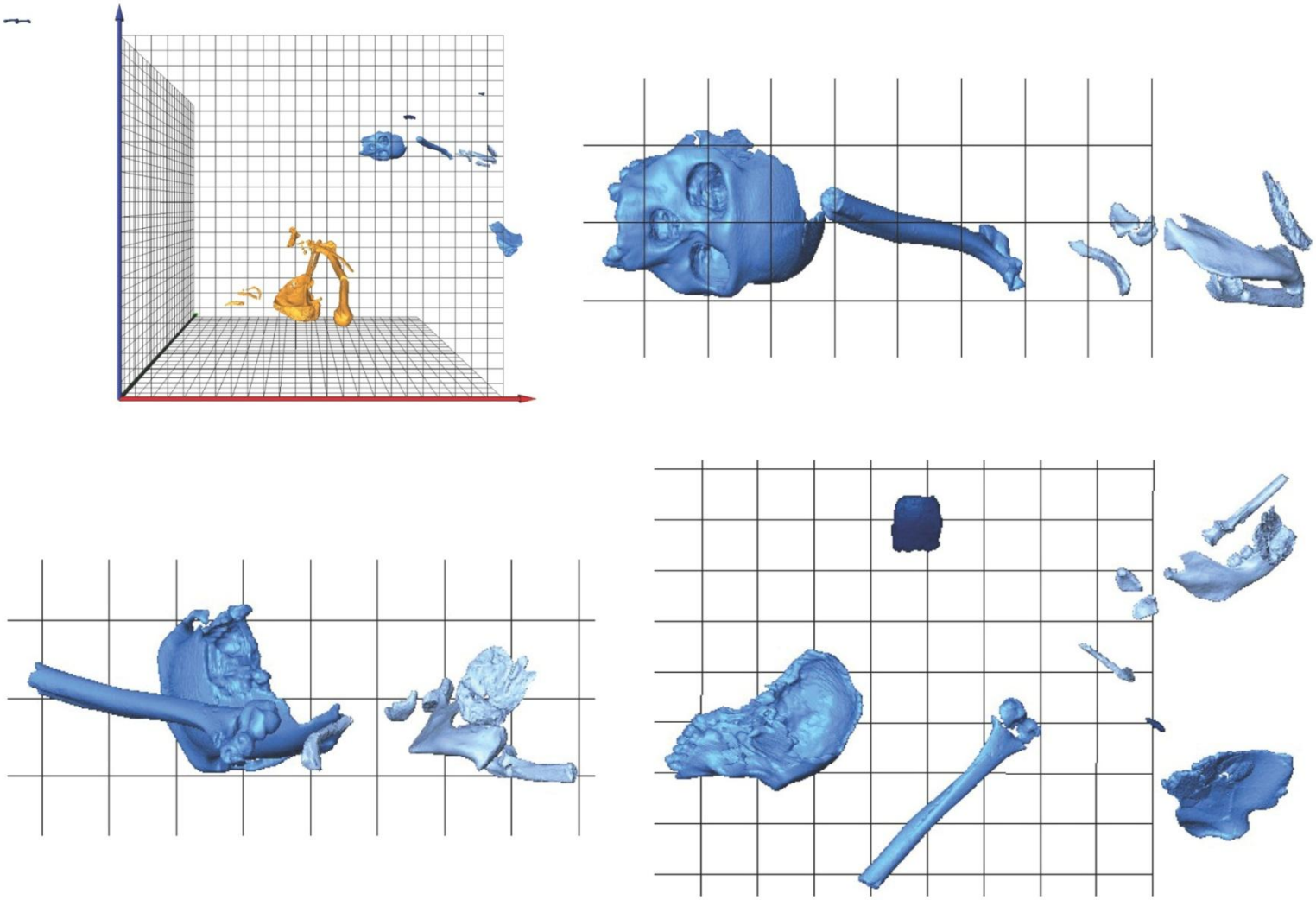
Top left: XZ view (from the south); top right: zoom of the XZ view; bottom left: zoom of the YZ view (from the east); bottom right: zoom of the XY view (from the top)

**Hypothesis 3**



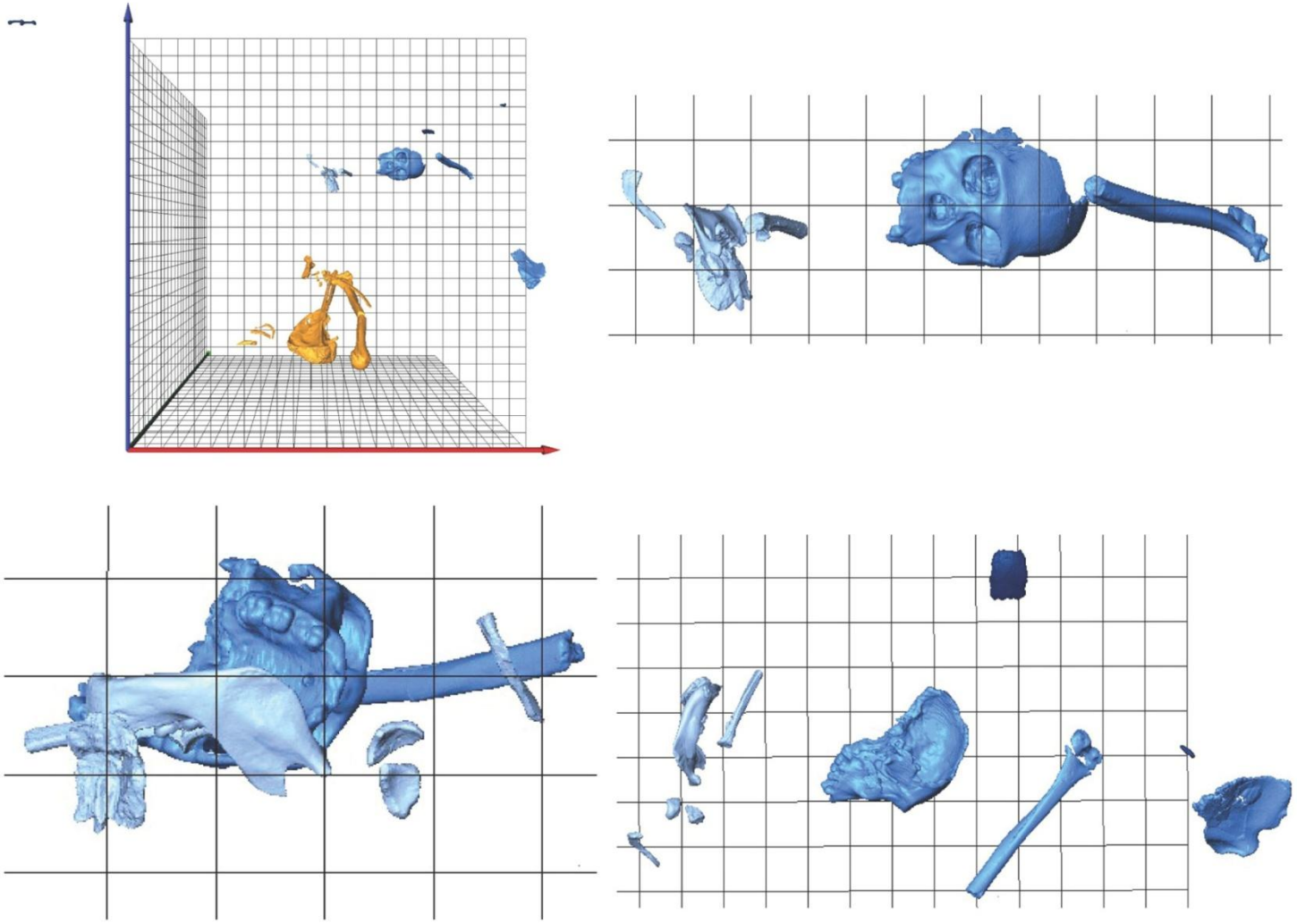
Top left: XZ view (from the south); top right: zoom of the XZ view; bottom left: zoom of the YZ view (from the east); bottom right: zoom of the XY view (from the top).

**Hypothesis 4**



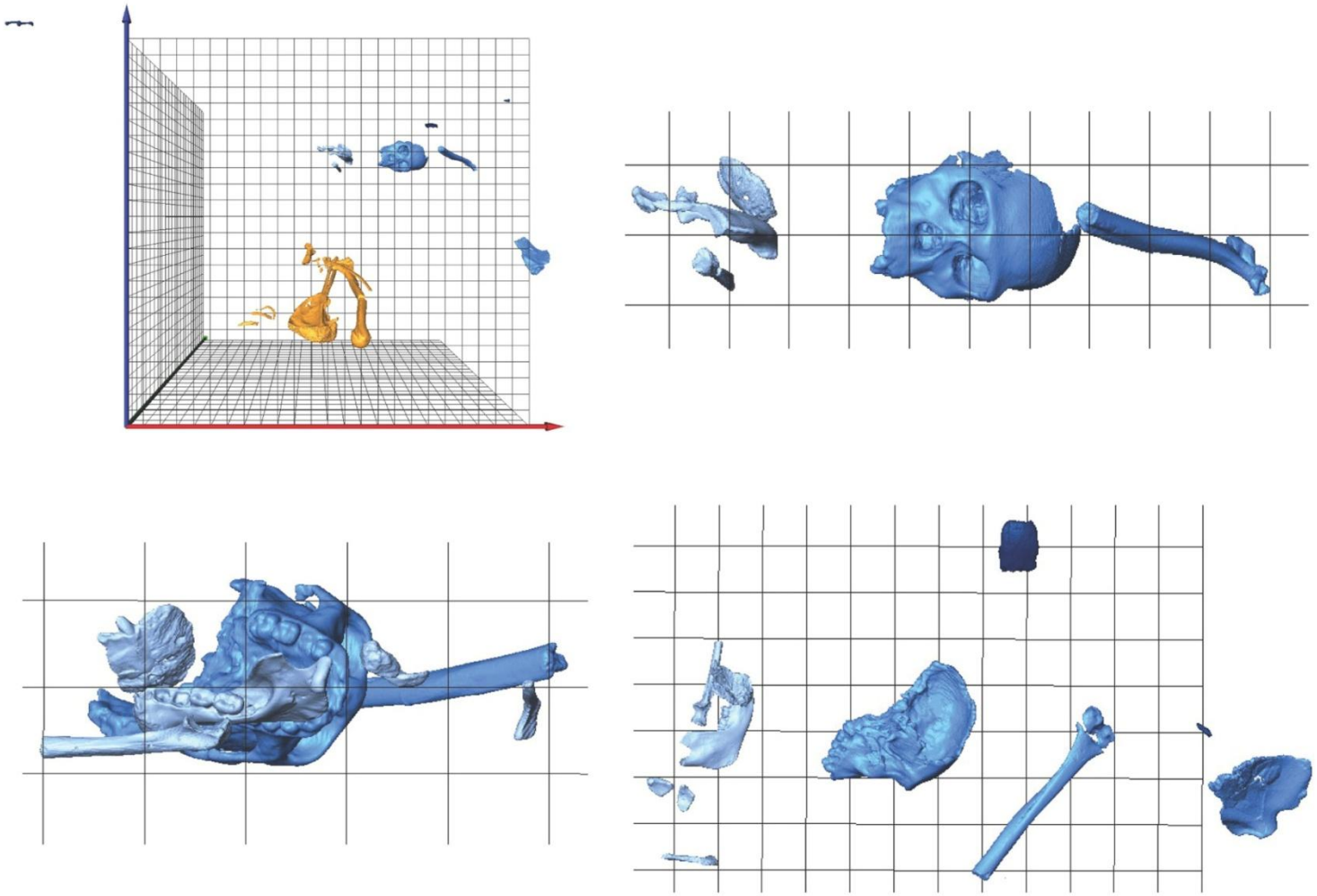
Top left: XZ view (from the south); top right: zoom of the XZ view; bottom left: zoom of the YZ view (from the east); bottom right: zoom of the XY view (from the top).

**Hypothesis 5**



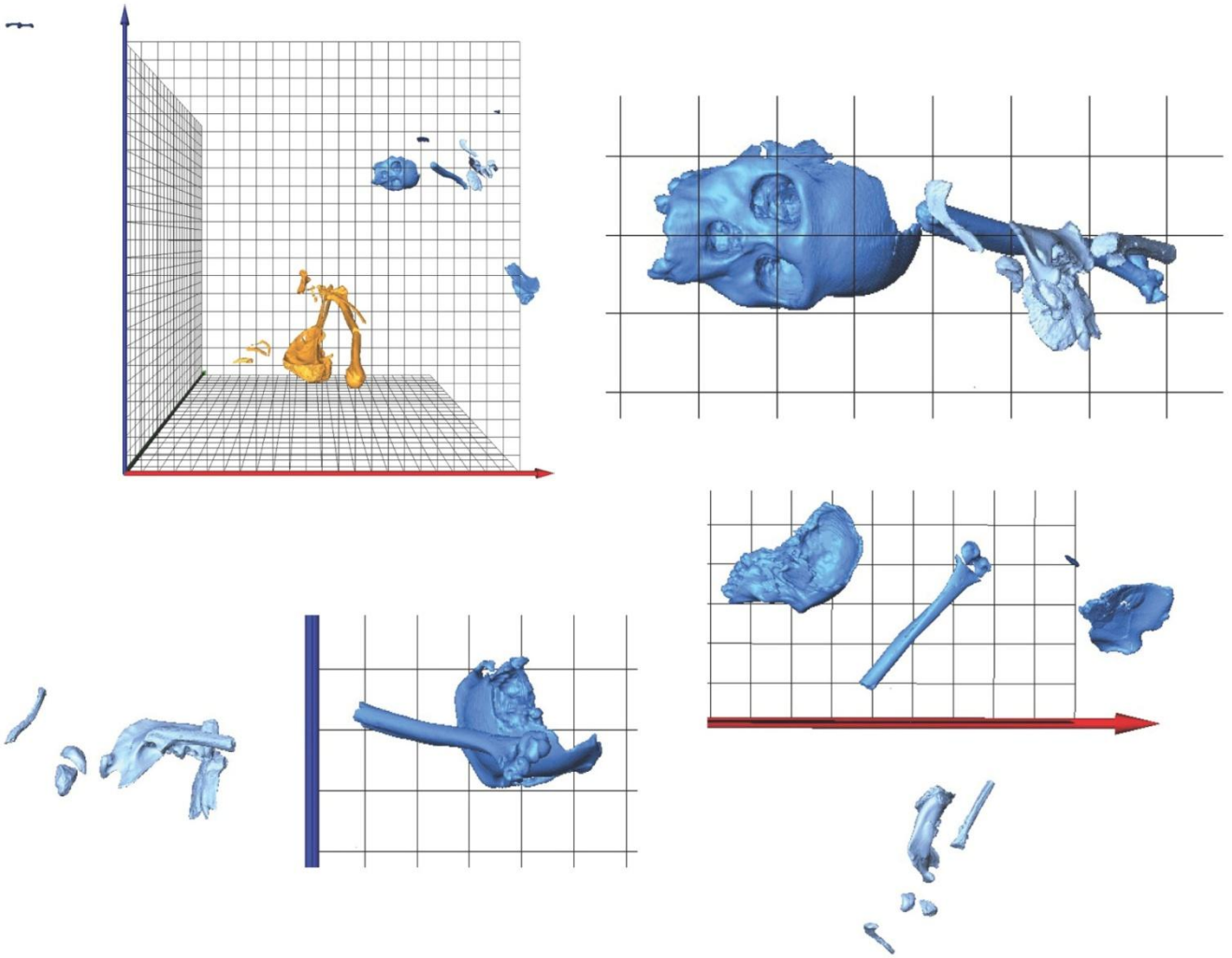
Top left: XZ view (from the south); top right: zoom of the XZ view; bottom left: zoom of the YZ view (from the east); bottom right: zoom of the XY view (from the top).

**Hypothesis 6**



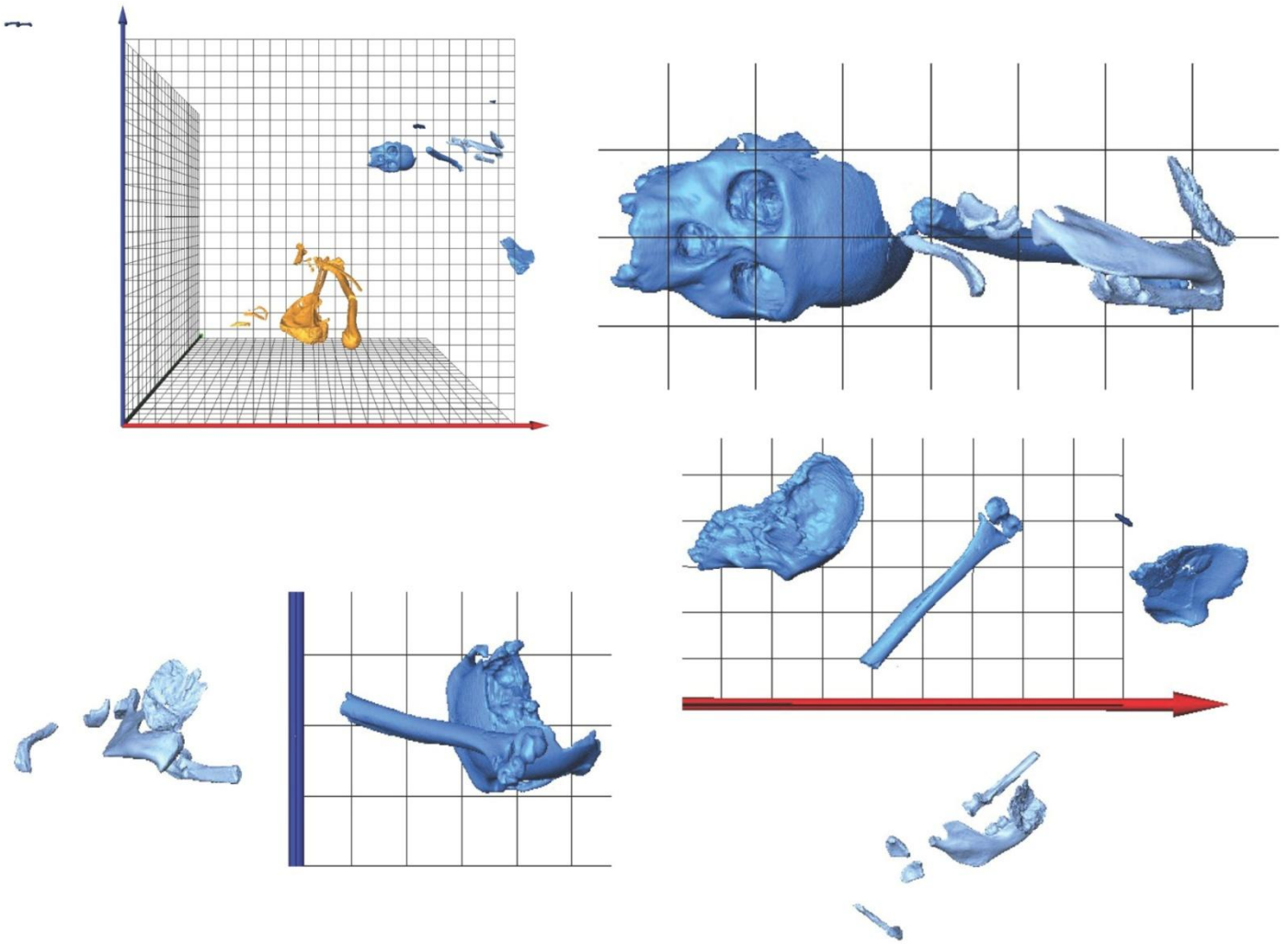
Top left: XZ view (from the south); top right: zoom of the XZ view; bottom left: zoom of the YZ view (from the east); bottom right: zoom of the XY view (from the top).

**Hypothesis 7**



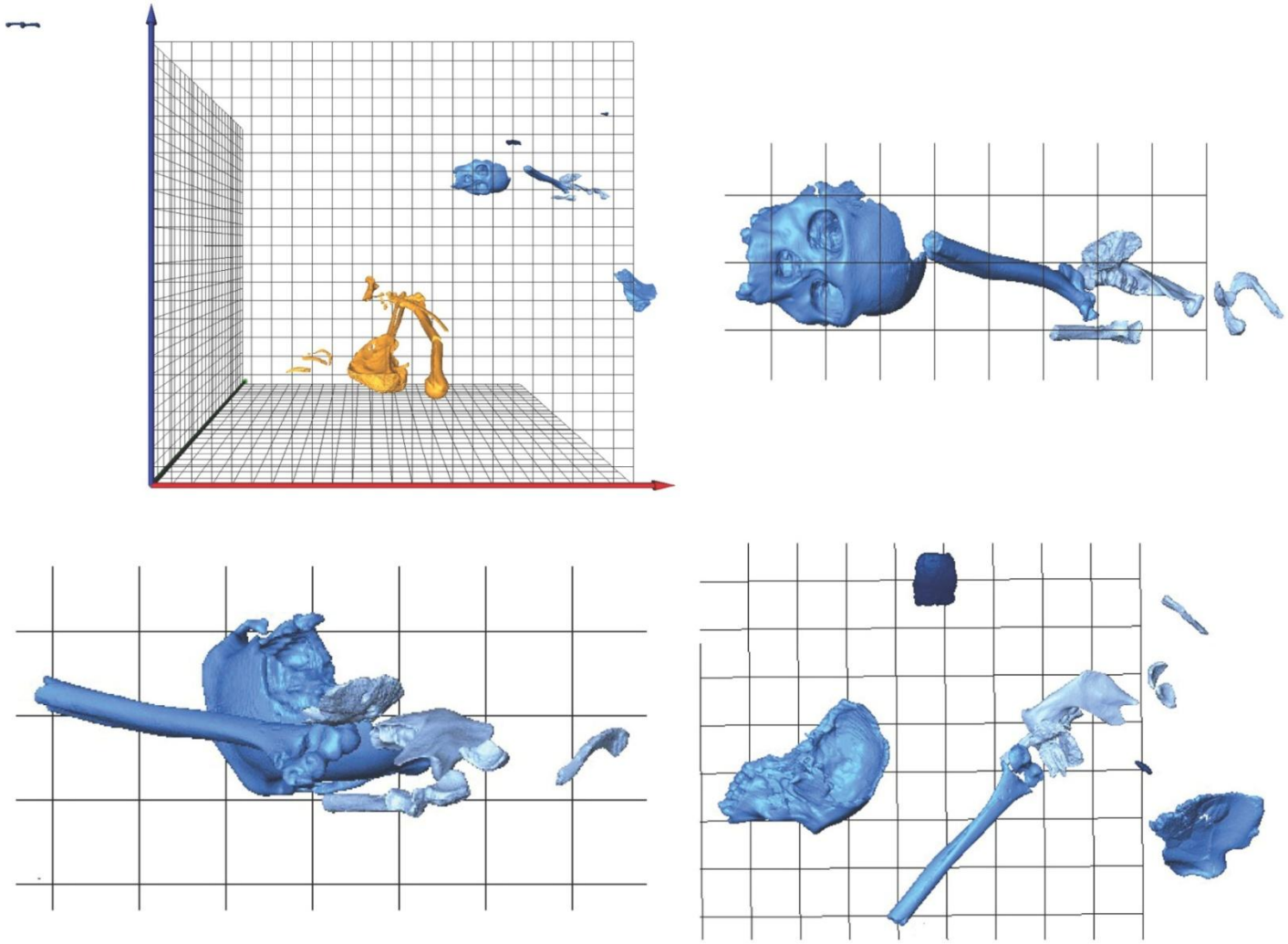
Top left: XZ view (from the south); top right: zoom of the XZ view; bottom left: zoom of the YZ view (from the east); bottom right: zoom of the XY view (from the top).

**Hypothesis 8**



Top left: XZ view (from the south); top right: zoom of the XZ view; bottom left: zoom of the YZ view (from the east); bottom right: zoom of the XY view (from the top).

**Hypothesis 9**



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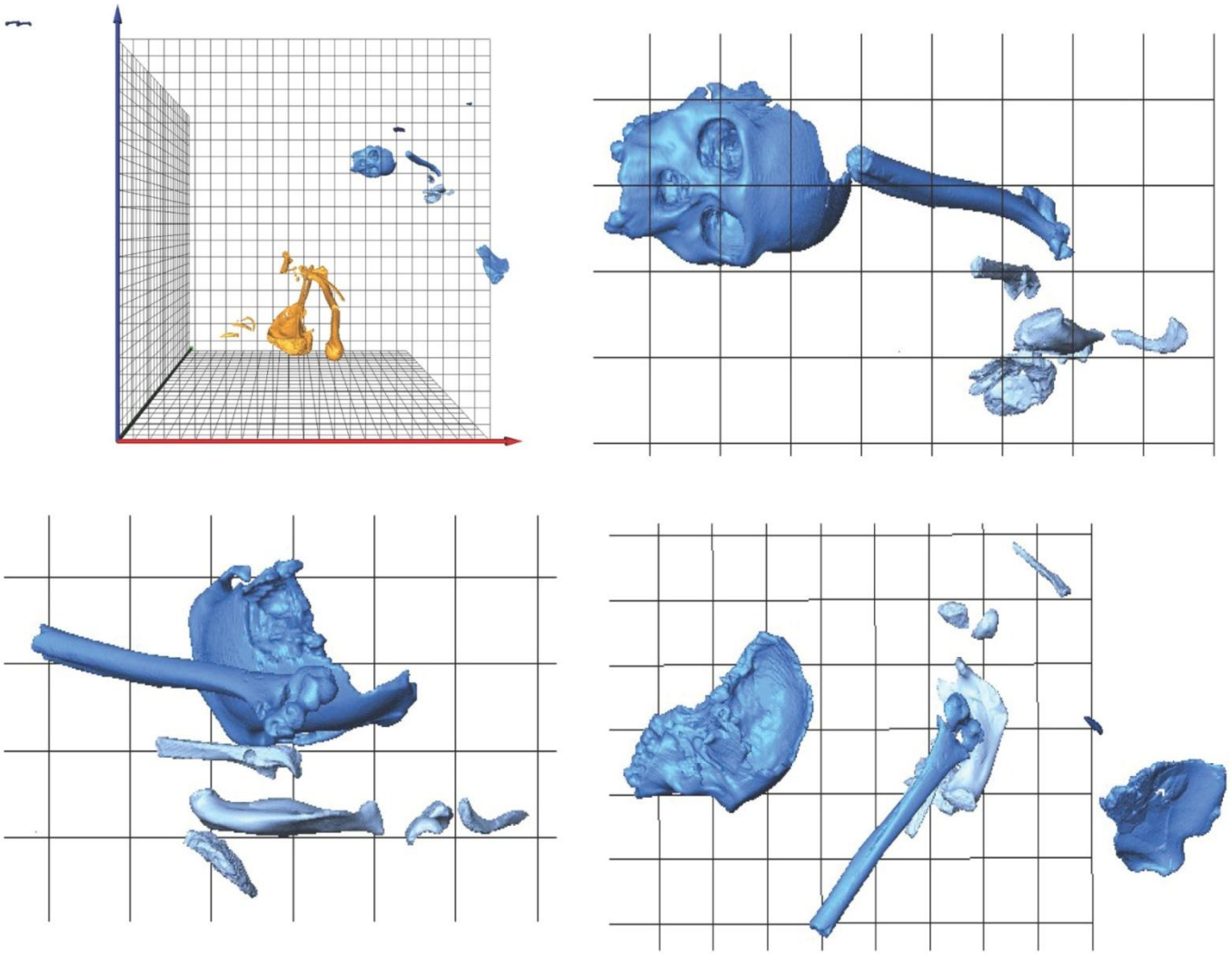
**Hypothesis 10**



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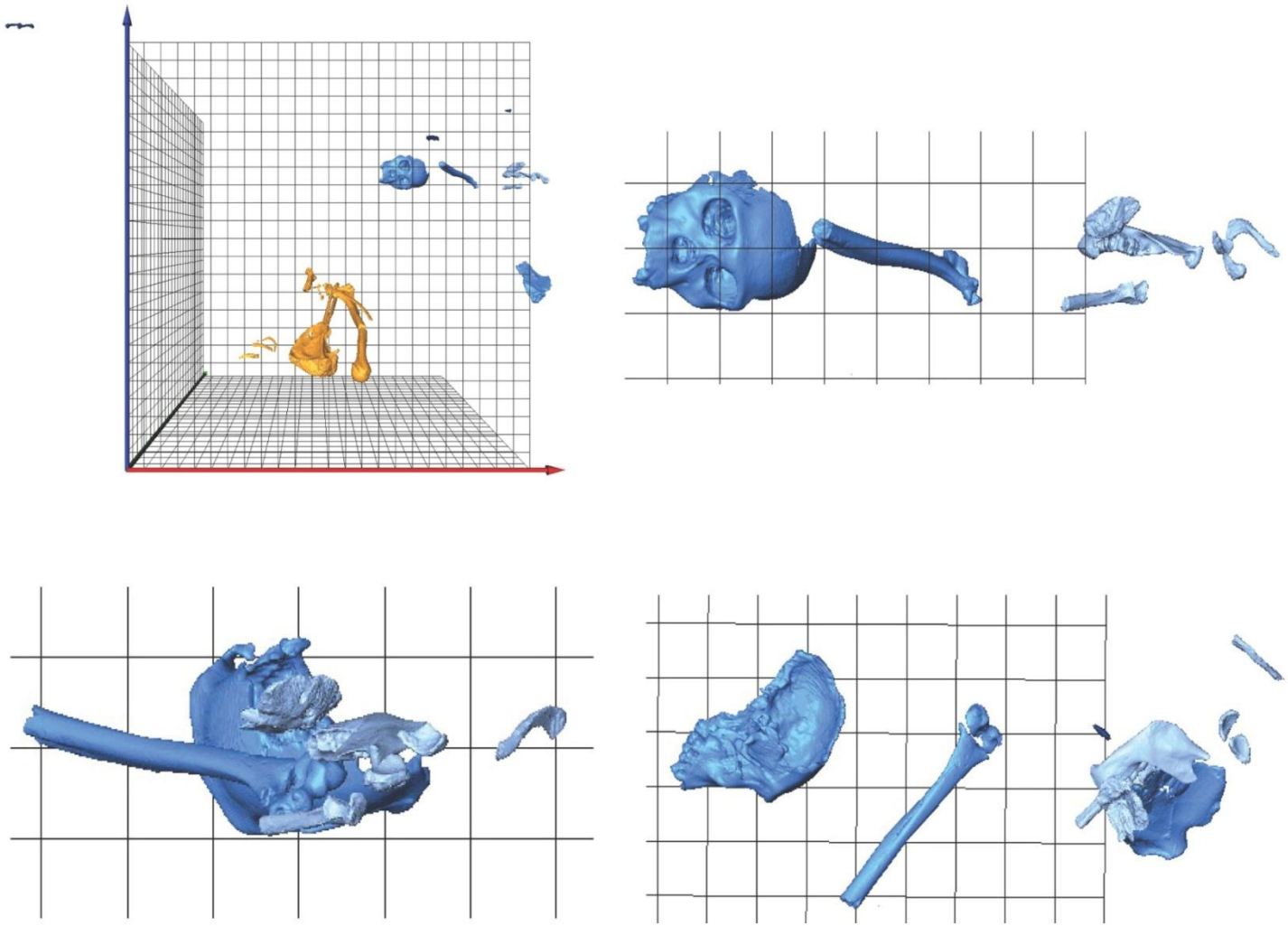
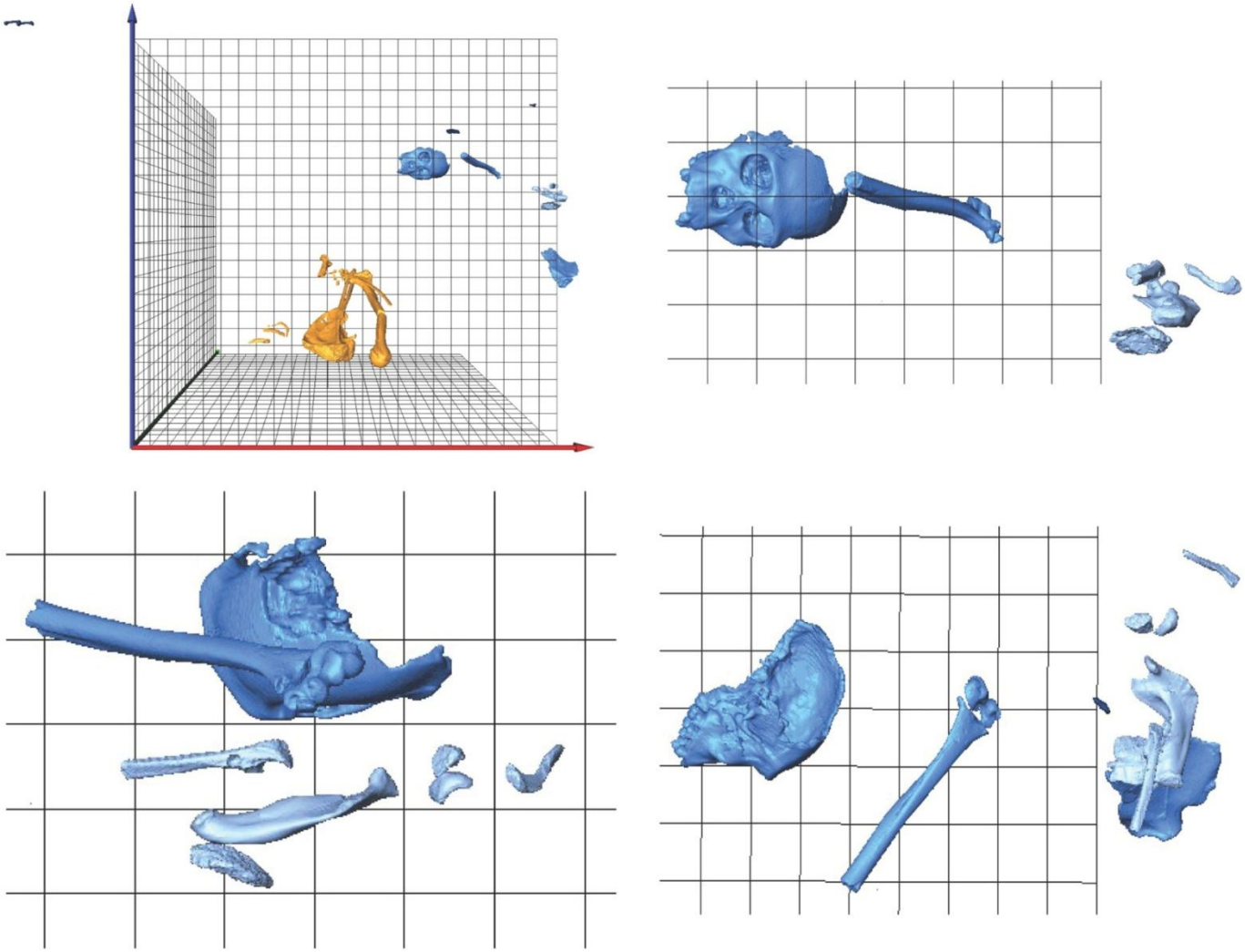
**Hypothesis 11**



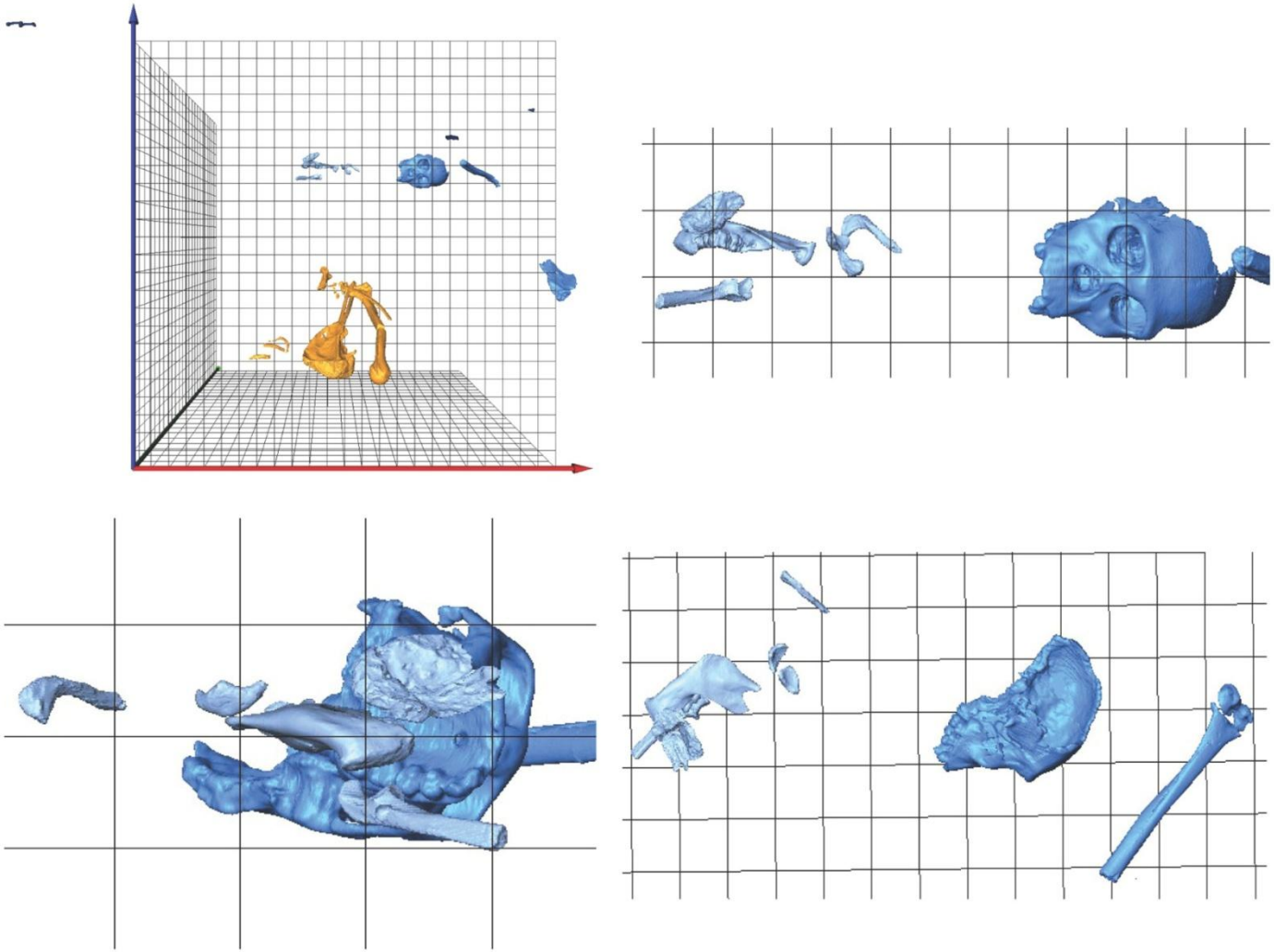
Top left: XZ view (from the south); top right: zoom of the XZ view; bottom left: zoom of the YZ view (from the east); bottom right: zoom of the XY view (from the top).

**Hypothesis 12**



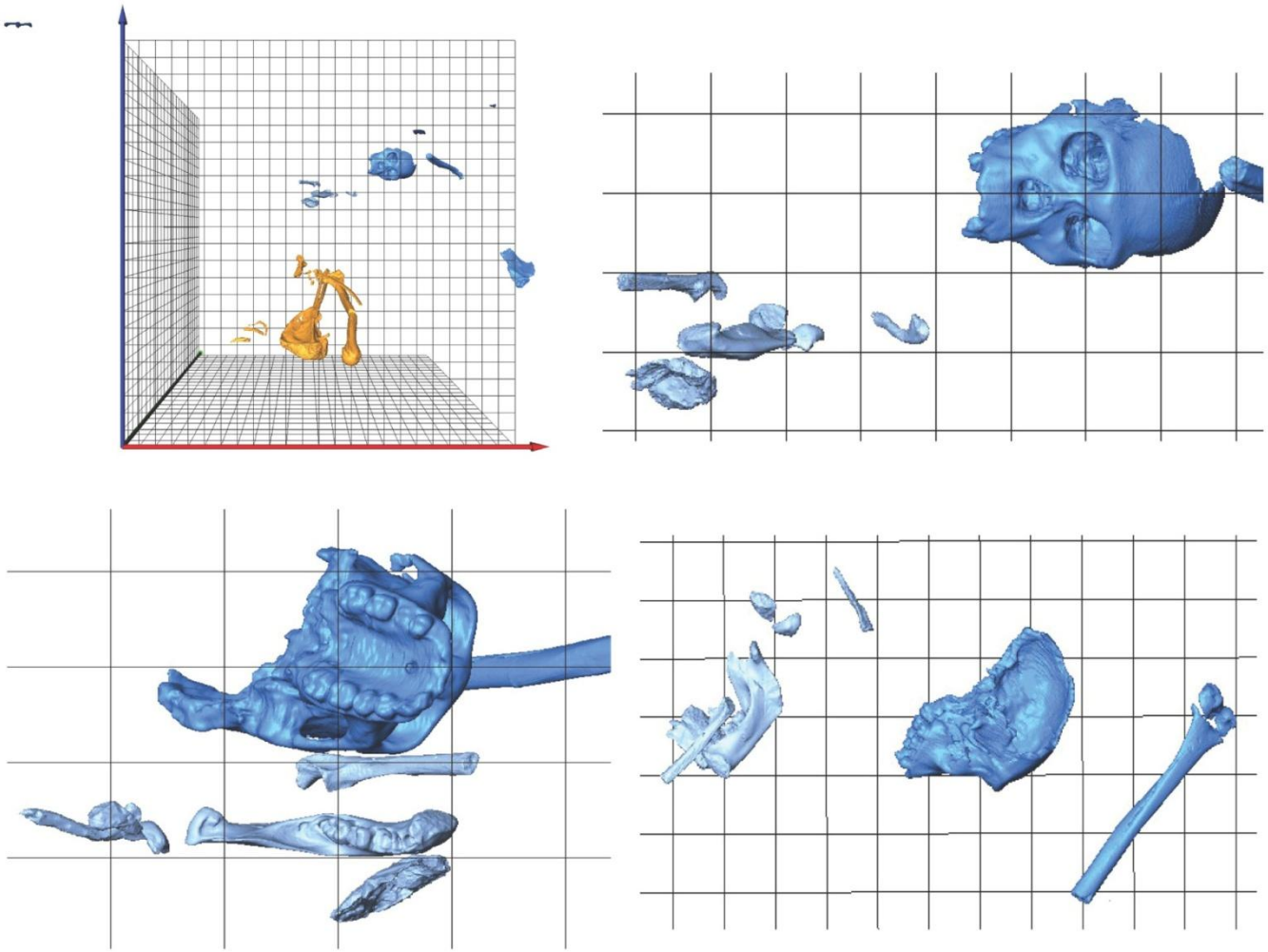
Top left: XZ view (from the south); top right: zoom of the XZ view; bottom left: zoom of the YZ view (from the east); bottom right: zoom of the XY view (from the top).

**Hypothesis 13**



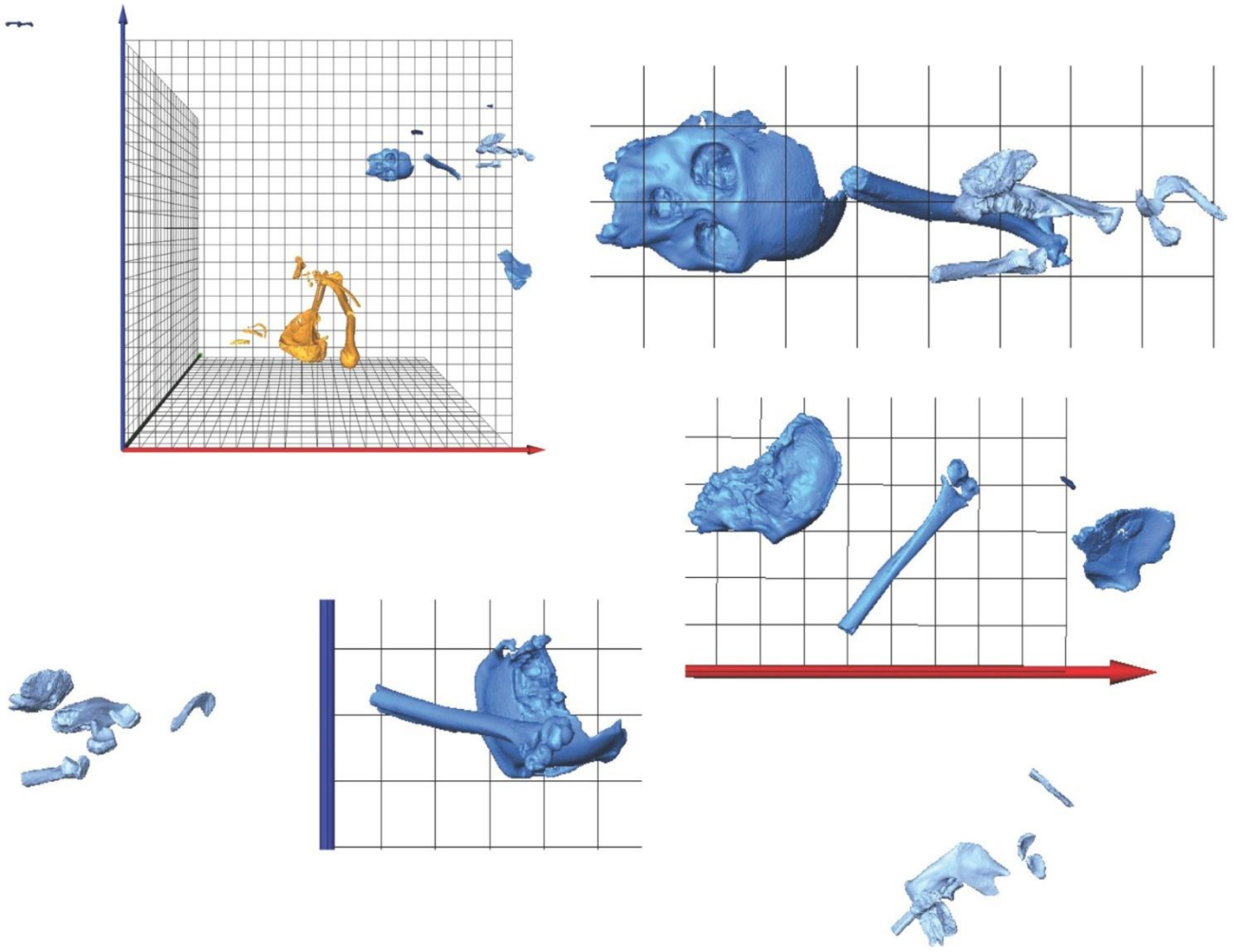
Top left: XZ view (from the south); top right: zoom of the XZ view; bottom left: zoom of the YZ view (from the east); bottom right: zoom of the XY view (from the top).

**Hypothesis 14**



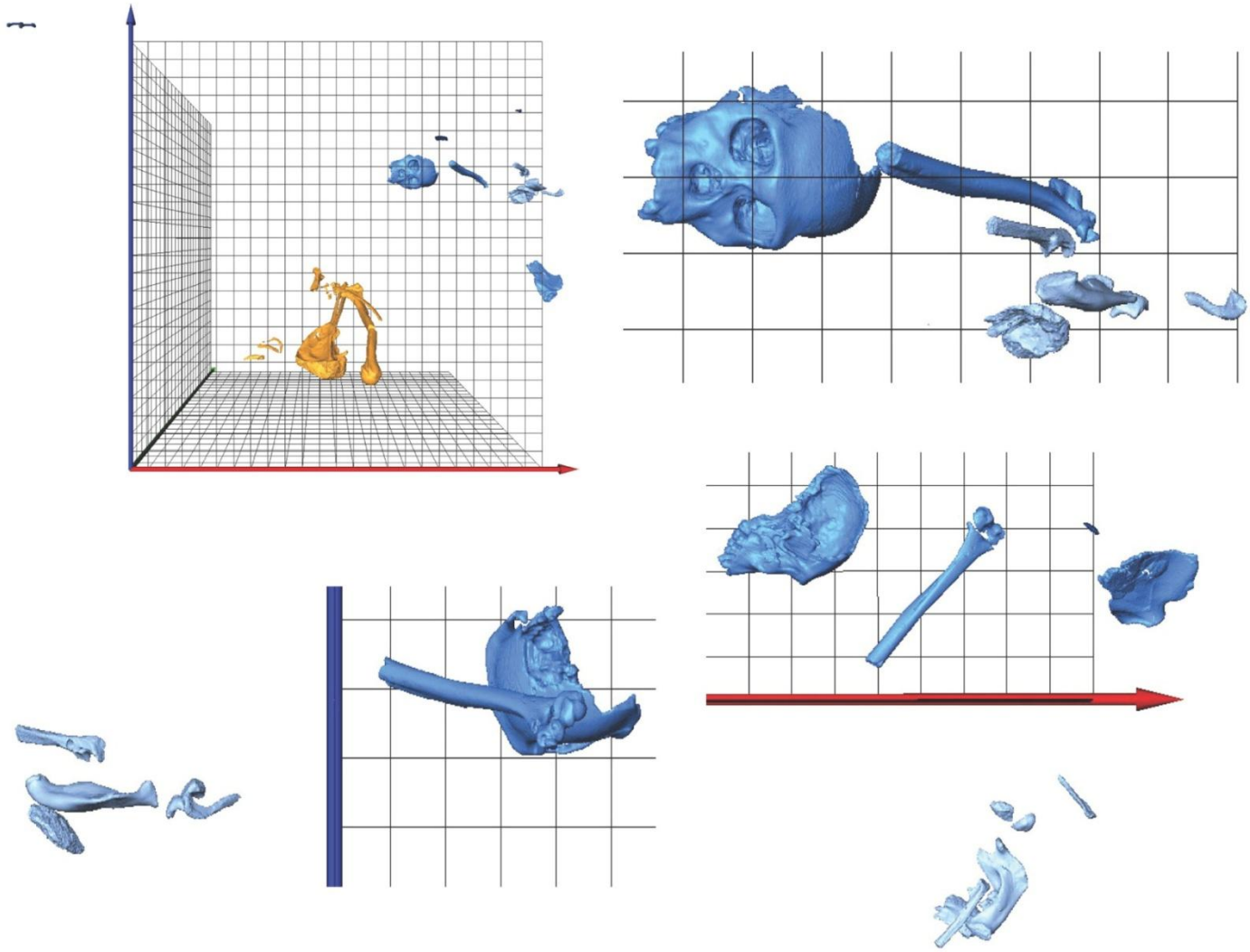
Top left: XZ view (from the south); top right: zoom of the XZ view; bottom left: zoom of the YZ view (from the east); bottom right: zoom of the XY view (from the top).

**Hypothesis 15**



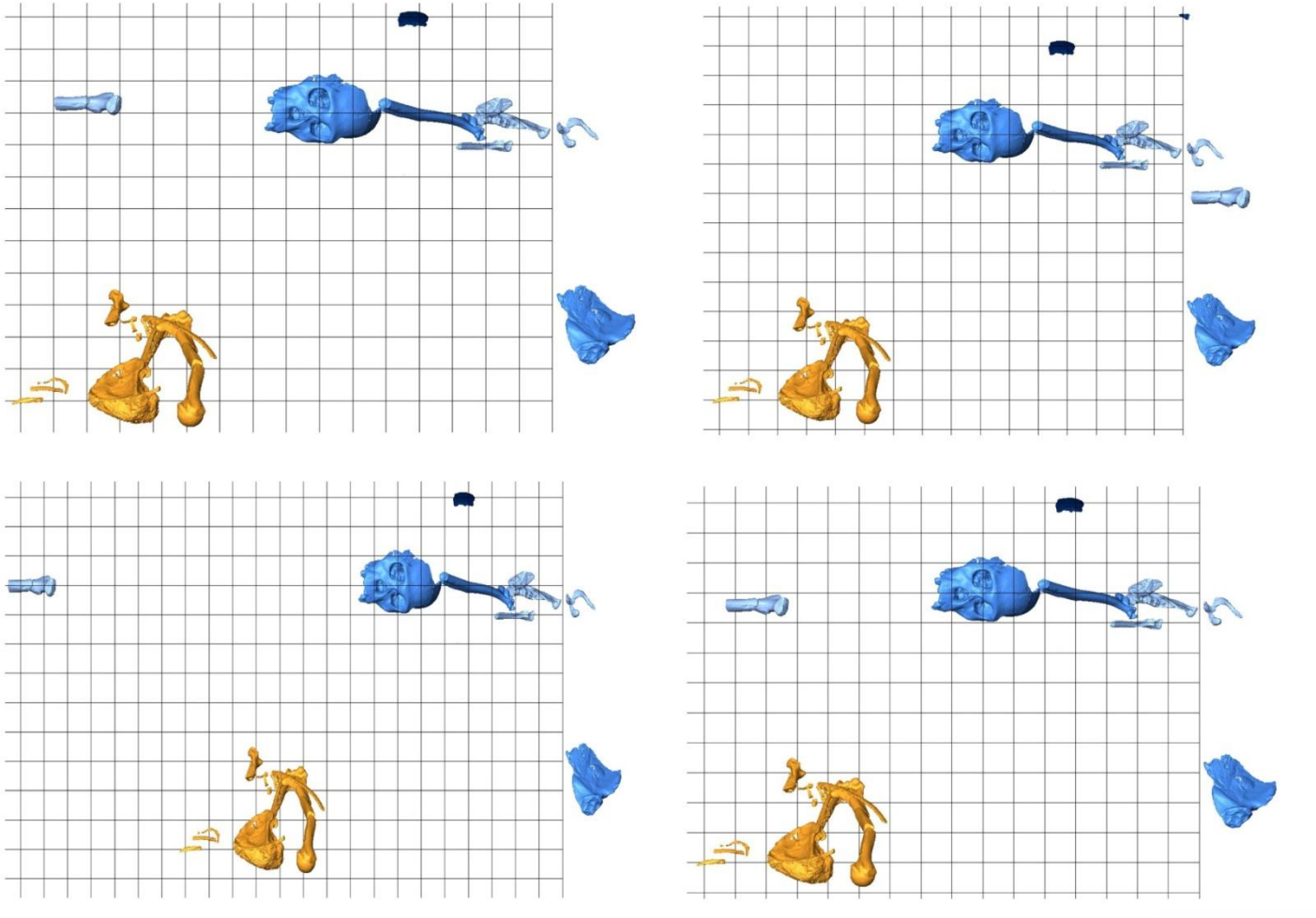
Top left: XZ view (from the south); top right: zoom of the XZ view; bottom left: zoom of the YZ view (from the east); bottom right: zoom of the XY view (from the top).

**Hypothesis 16**

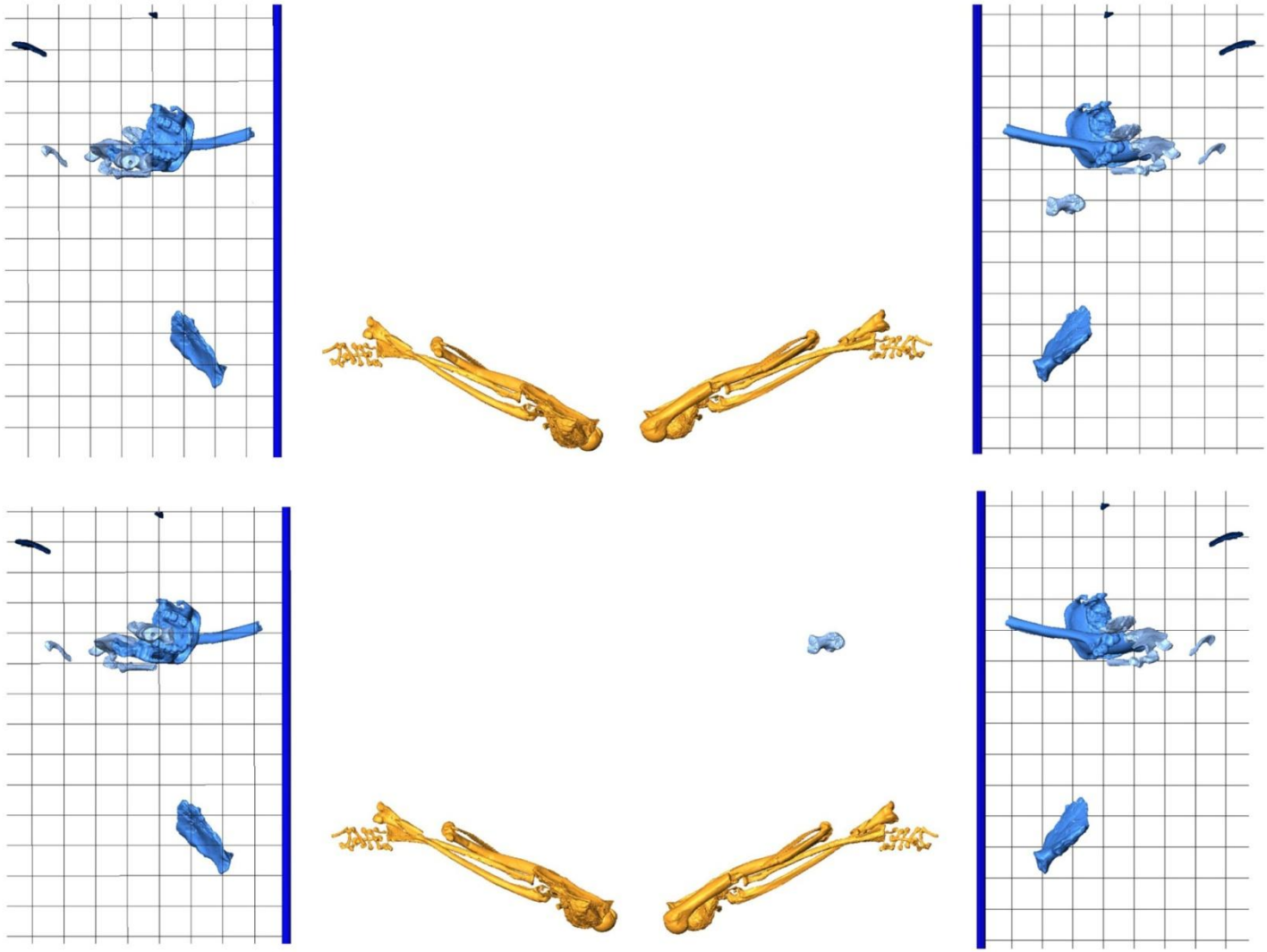


Top left: XZ view (from the south); top right: zoom of the XZ view; bottom left: zoom of the YZ view (from the east); bottom right: zoom of the XY view (from the top).

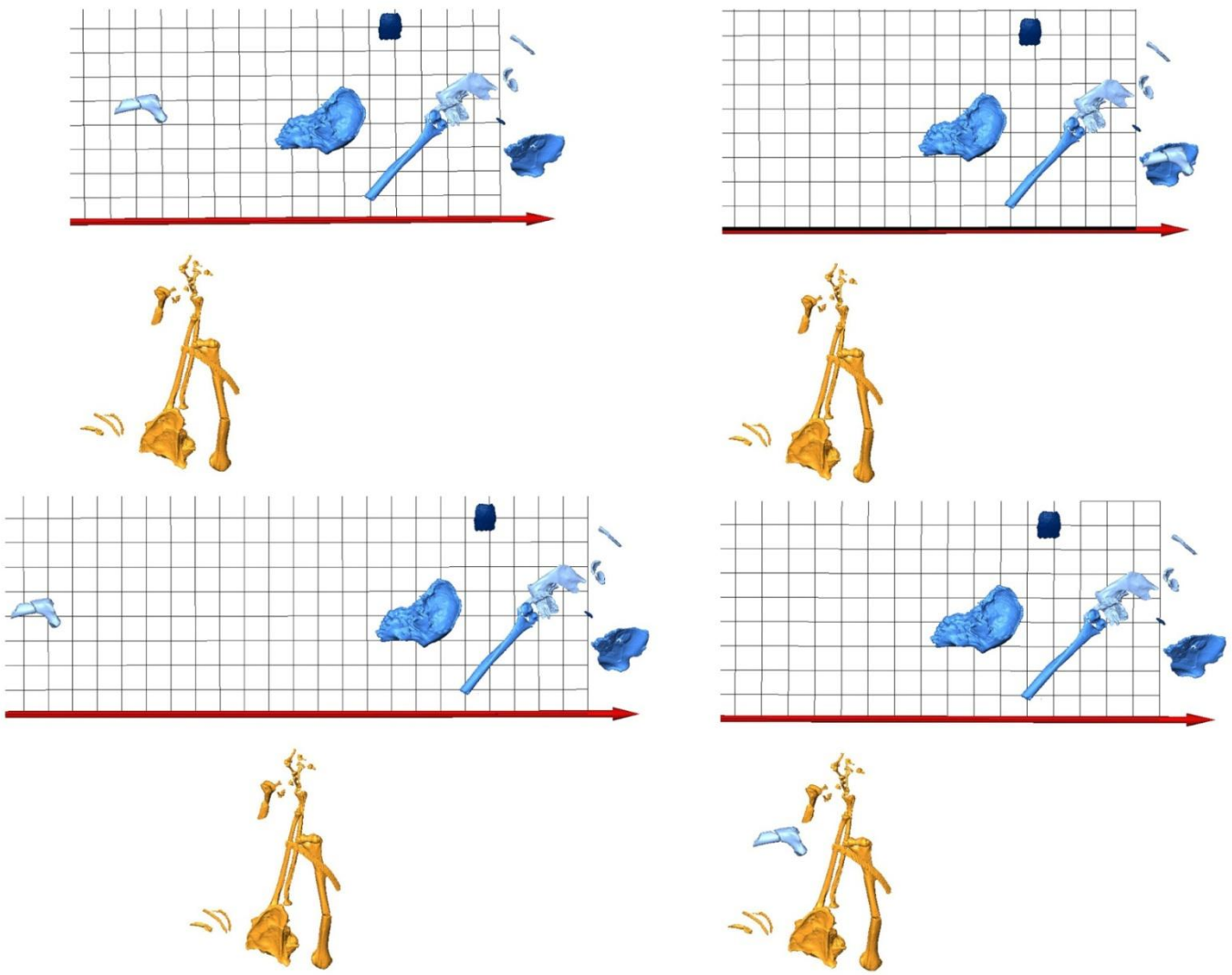
**Leg extended**



XZ view (from the south): no movement (top left), movement to the east (top right), movement to the west (bottom left) and movement to the south (bottom right).

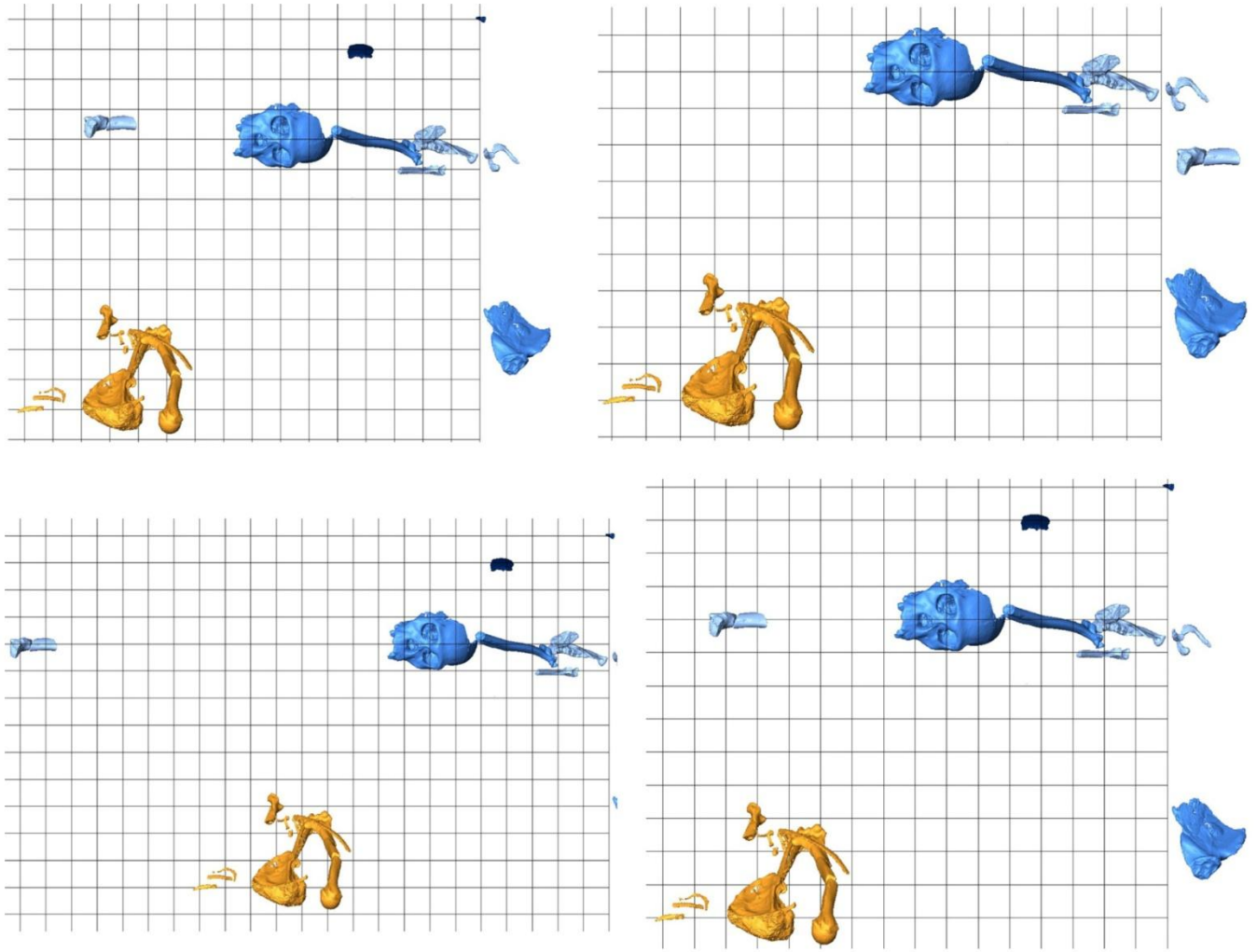


YZ view (from the west, images on the left; from the east, images on the right): no movement (top left), movement to the east (top right), movement to the west (bottom left) and movement to the south (bottom right).

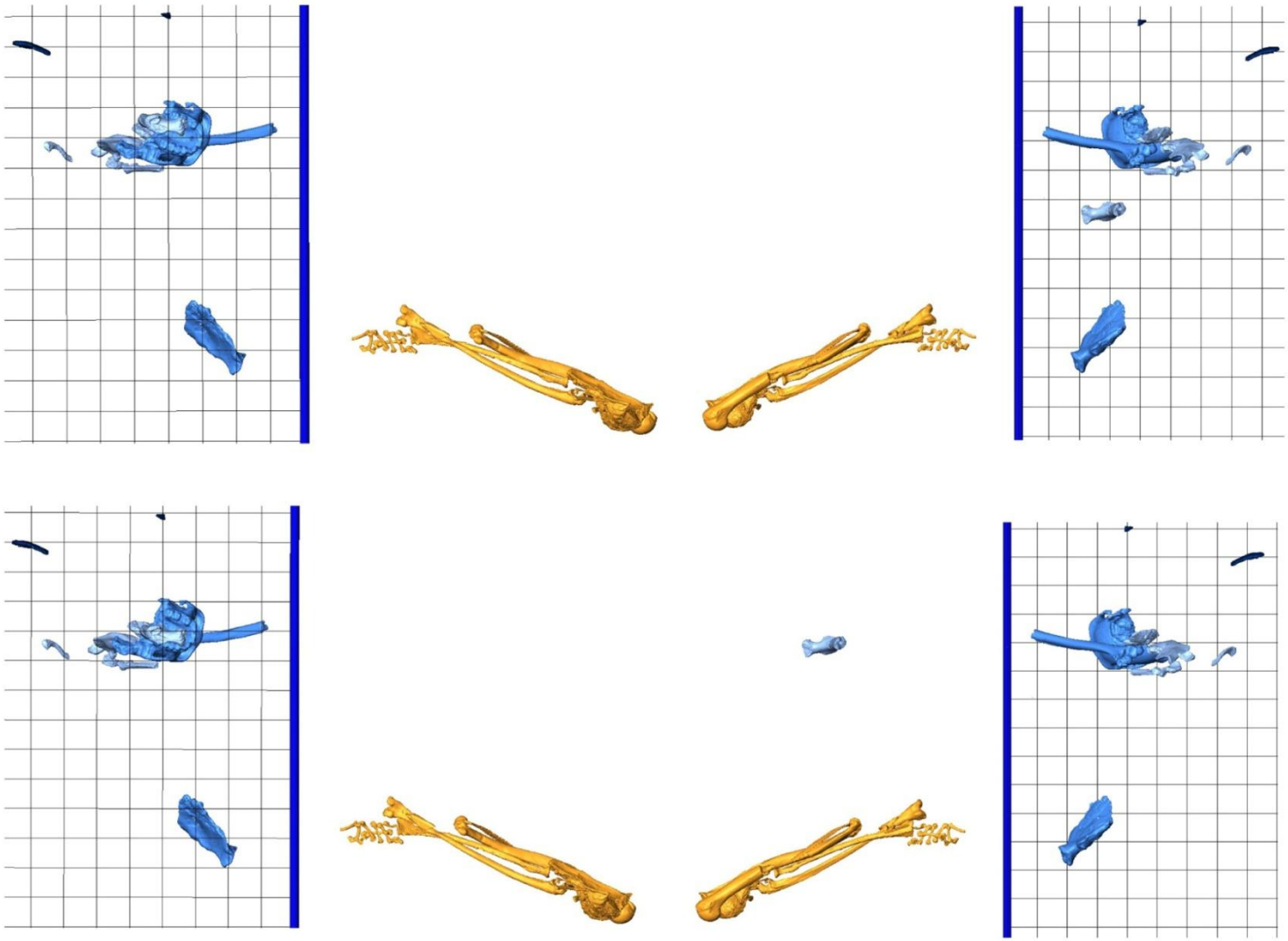


XY view (from the top): no movement (top left), movement to the east (top right), movement to the west (bottom left) and movement to the south (bottom right).

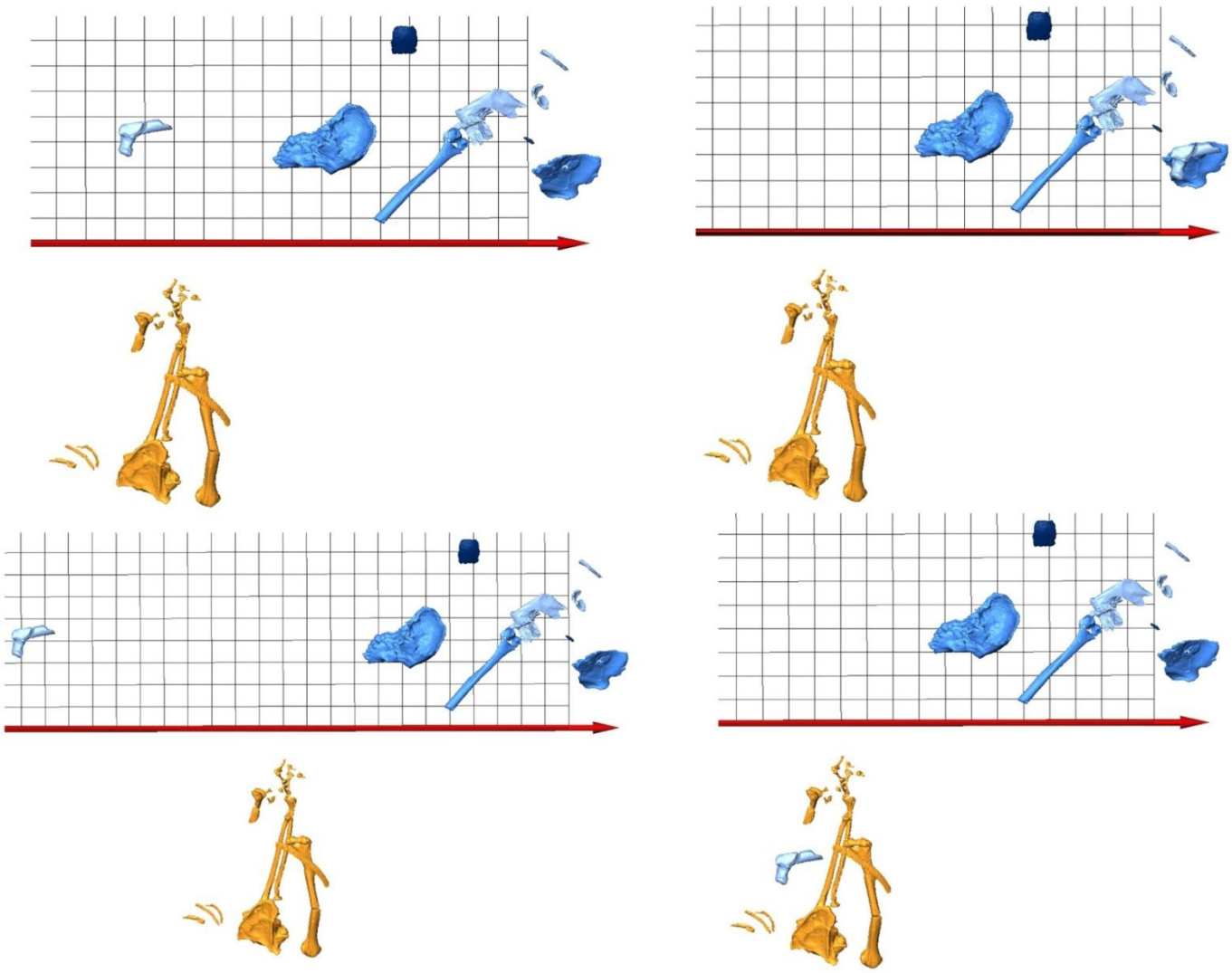
**Leg flexed**



XZ view (from the south): no movement (top left), movement to the east (top right), movement to the west (bottom left) and movement to the south (bottom right).

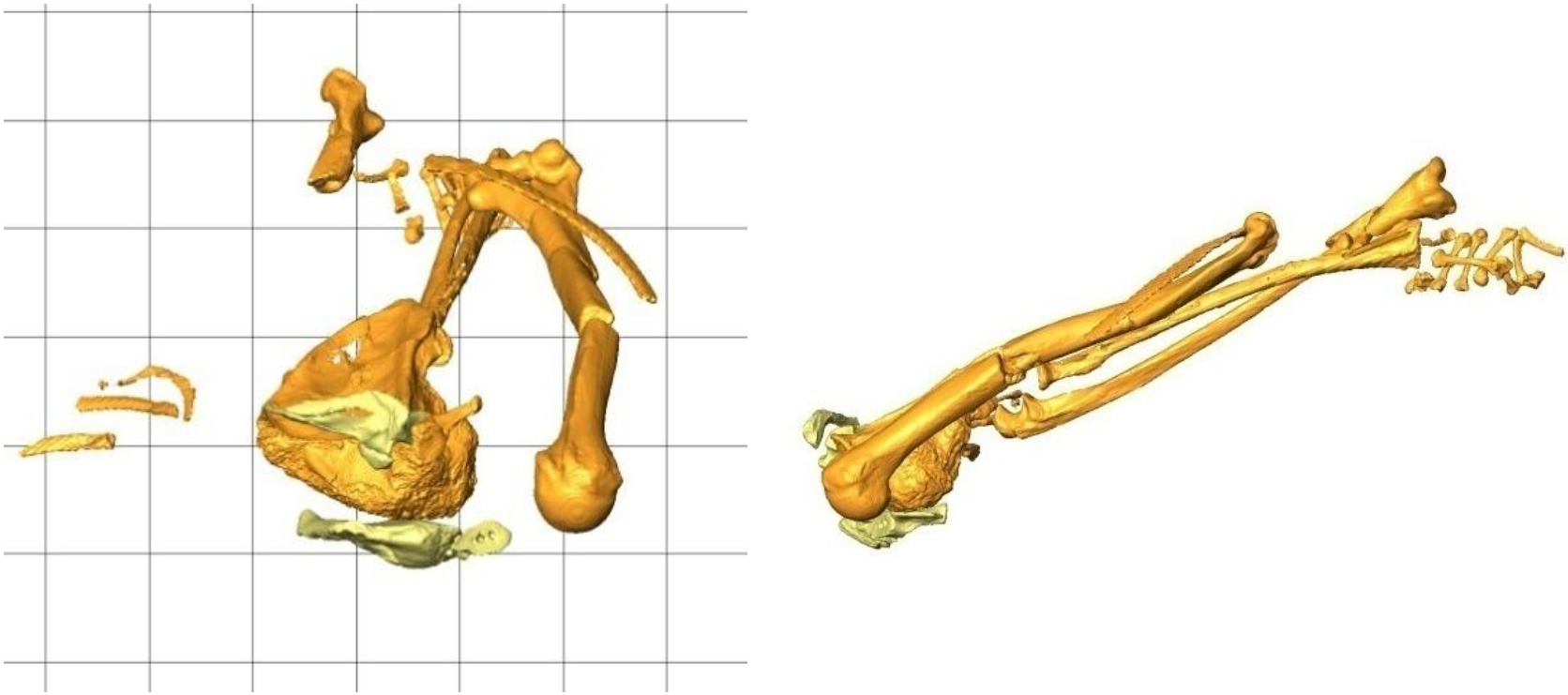


YZ view (from the west, images on the left; from the east, images on the right): no movement (top left), movement to the east (top right), movement to the west (bottom left) and movement to the south (bottom right).



XY view (from the top): no movement (top left), movement to the east (top right), movement to the west (bottom left) and movement to the south (bottom right).

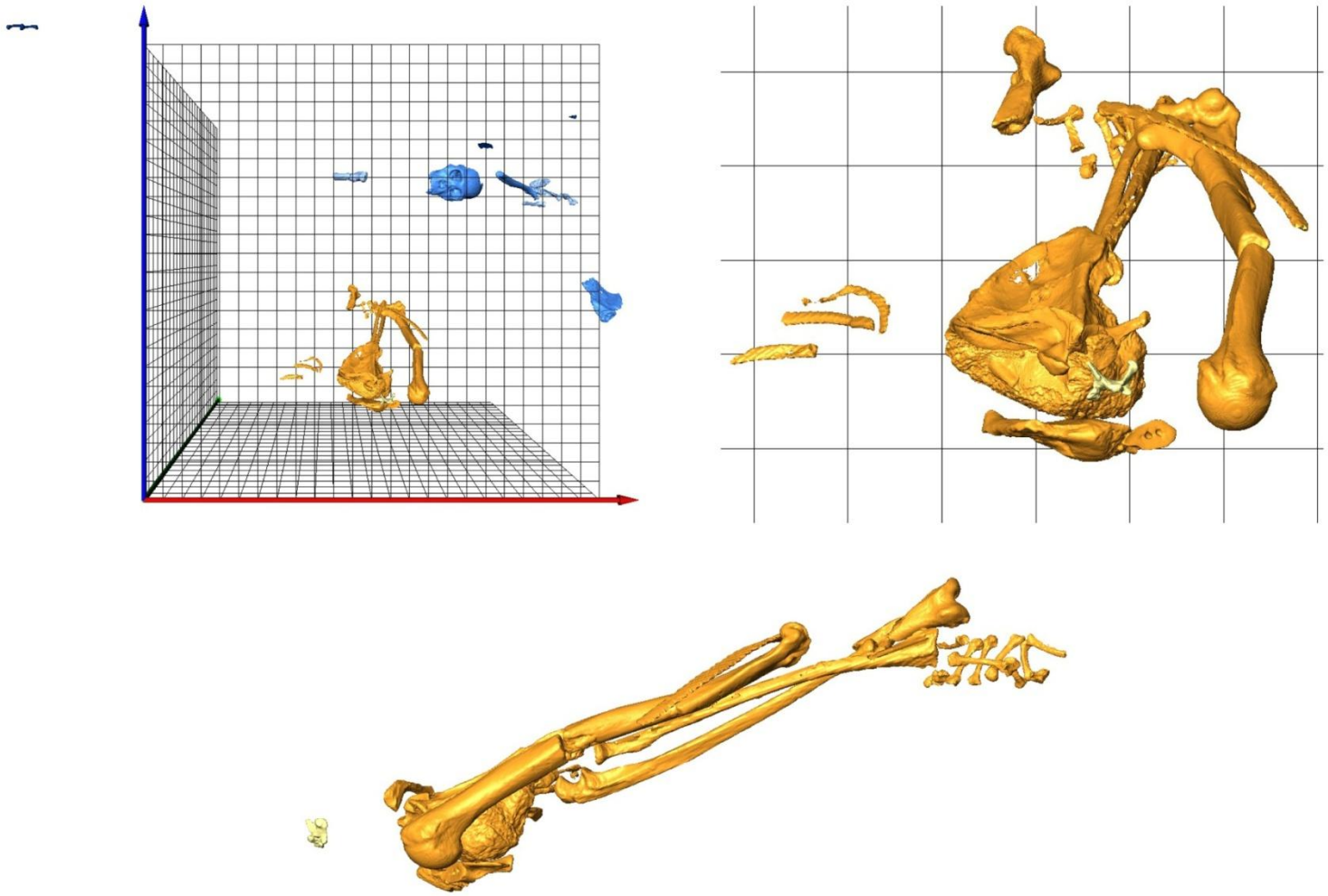
REFITTING MH2 ‘SCAPULA FRAGMENT BLOCK’



Left: XZ view (from the south); right: YZ view (from the east)

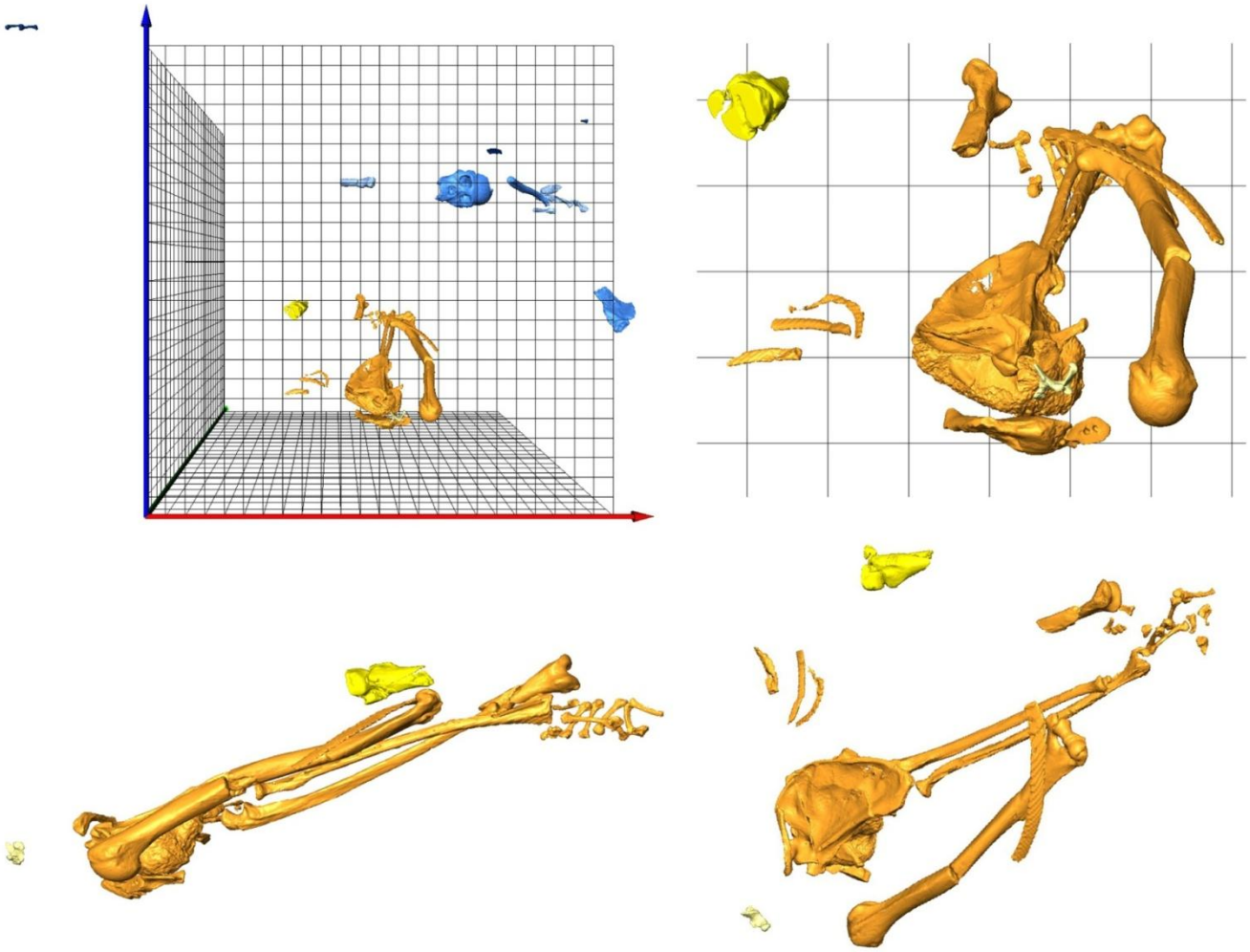
Remark: the scapula fragment, mandible and clavicle have been lightened in these figures picture to facilitate the understanding of the figure. In the final model, they are shown in the same color as the bones from the arm block, since their exact position is known.

REFITTING MH2 CERVICAL VERTEBRA (UW88-96)



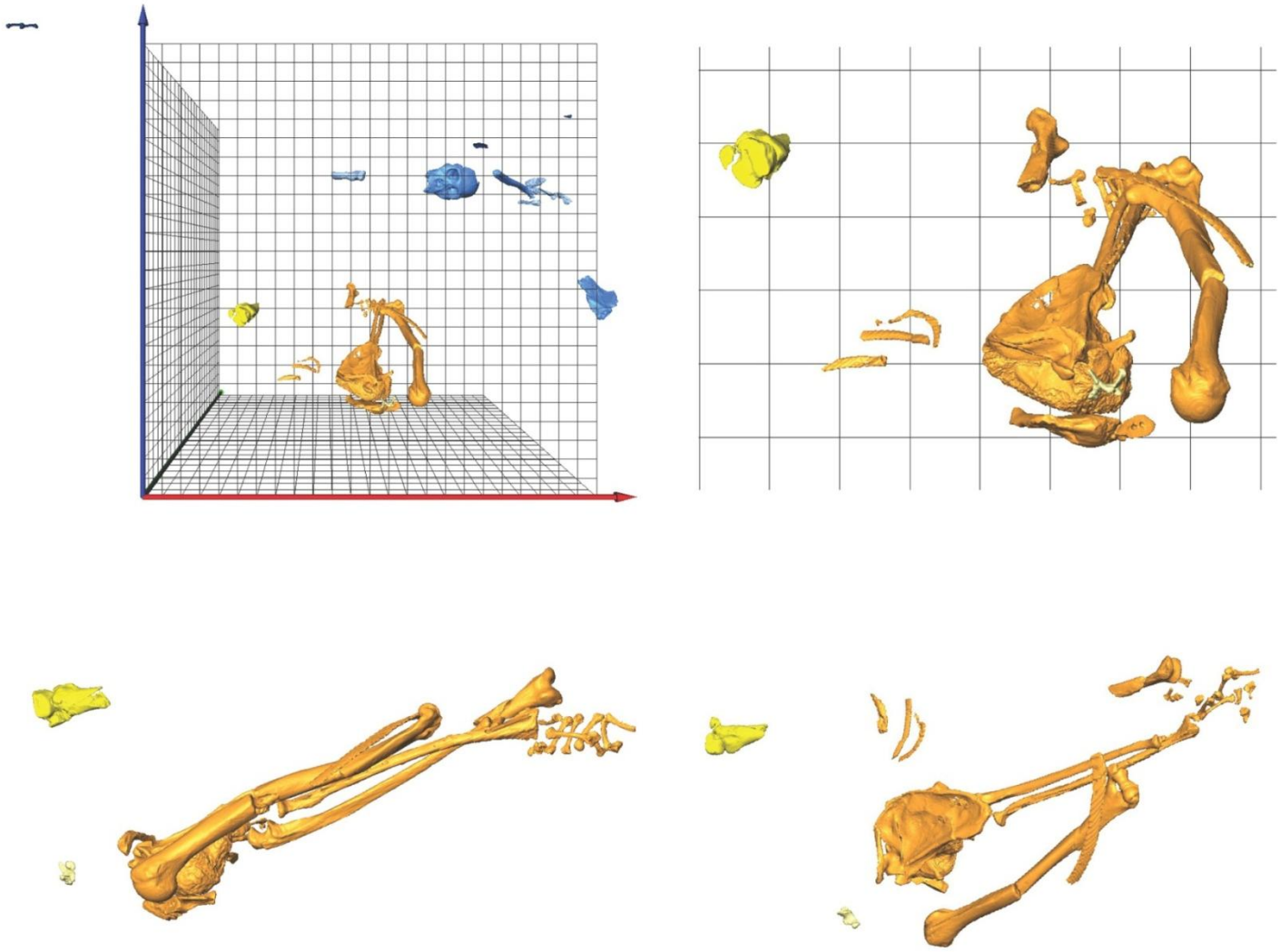
Top left: XZ view (from the south); top right: zoom of the XZ view (from the north); bottom: zoom of the YZ view (from the east).

**Hypothesis 1**



Top left: XZ view (from the south); top right: zoom of the XZ view (from the north); bottom left: YZ view (from the east); bottom: XY view (from the top).

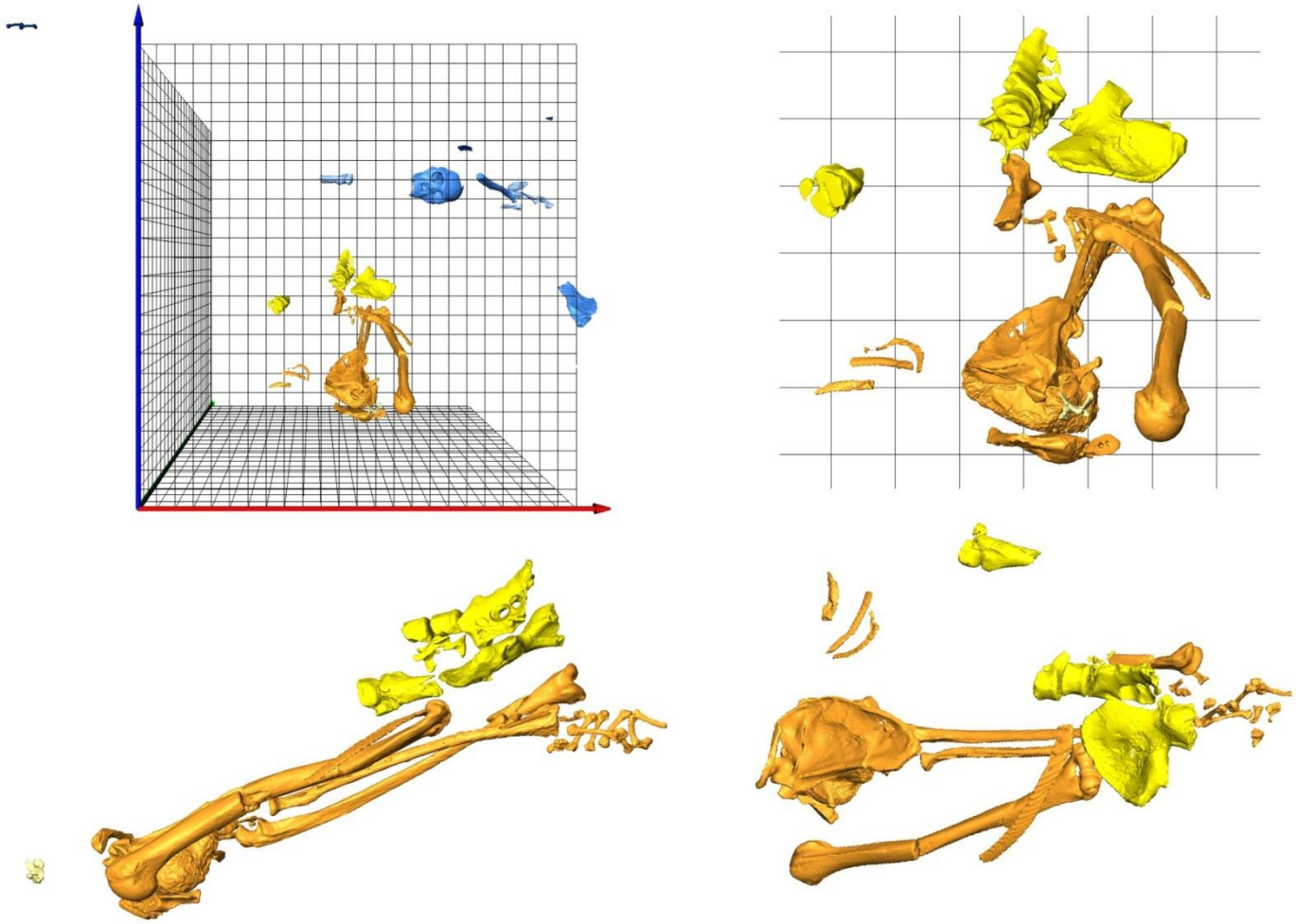
**Hypothesis 2**



Top left: XZ view (from the south); top right: zoom of the XZ view (from the north); bottom left: YZ view (from the east); bottom: XY view (from the top).

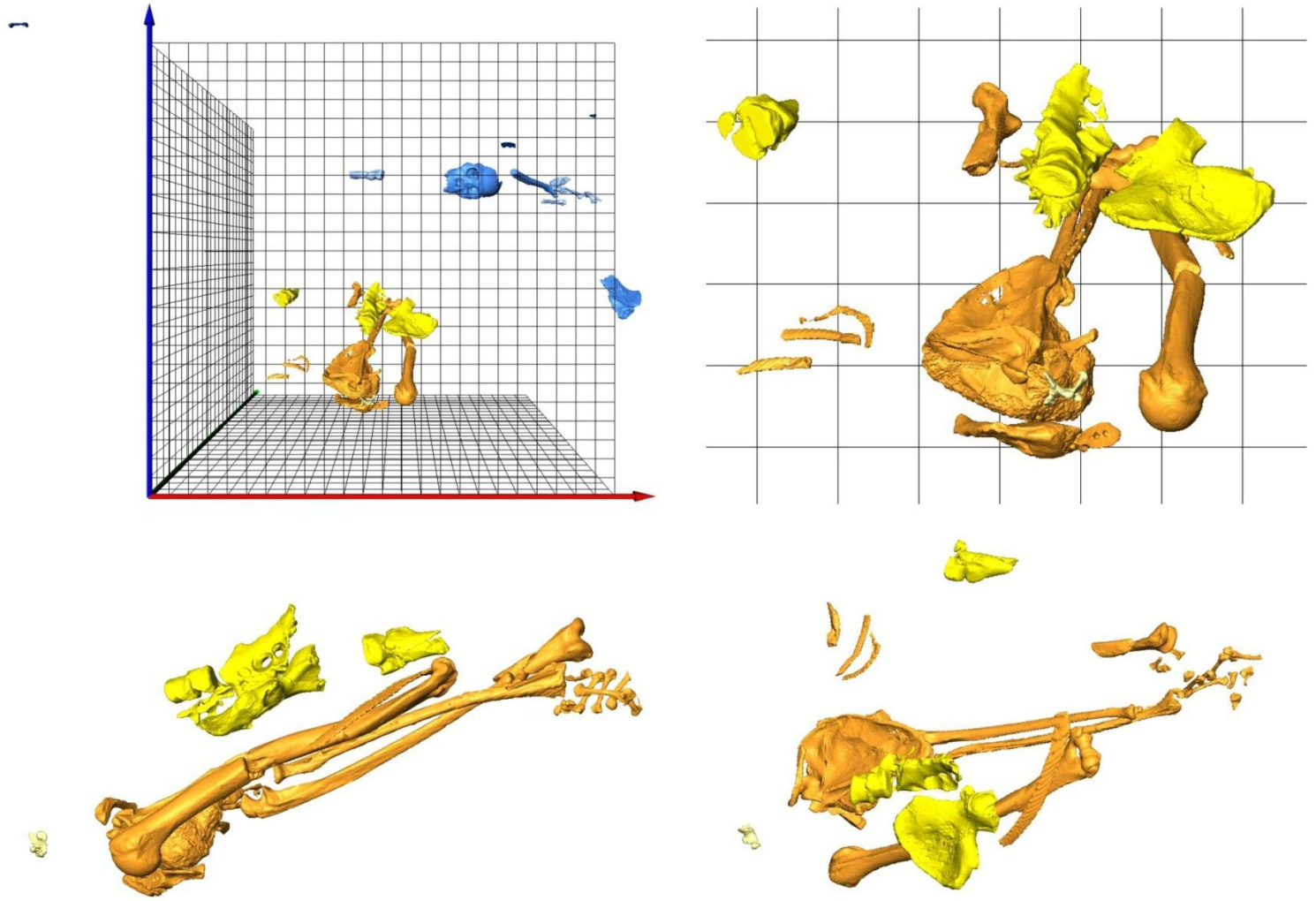
REFITTING MH2 SACRUM AND ILIUM

**Hypothesis 1**



Top left: XZ view (from the south); top right: zoom of the XZ view (from the north); bottom left: YZ view (from the east); bottom: XY view (from the top).

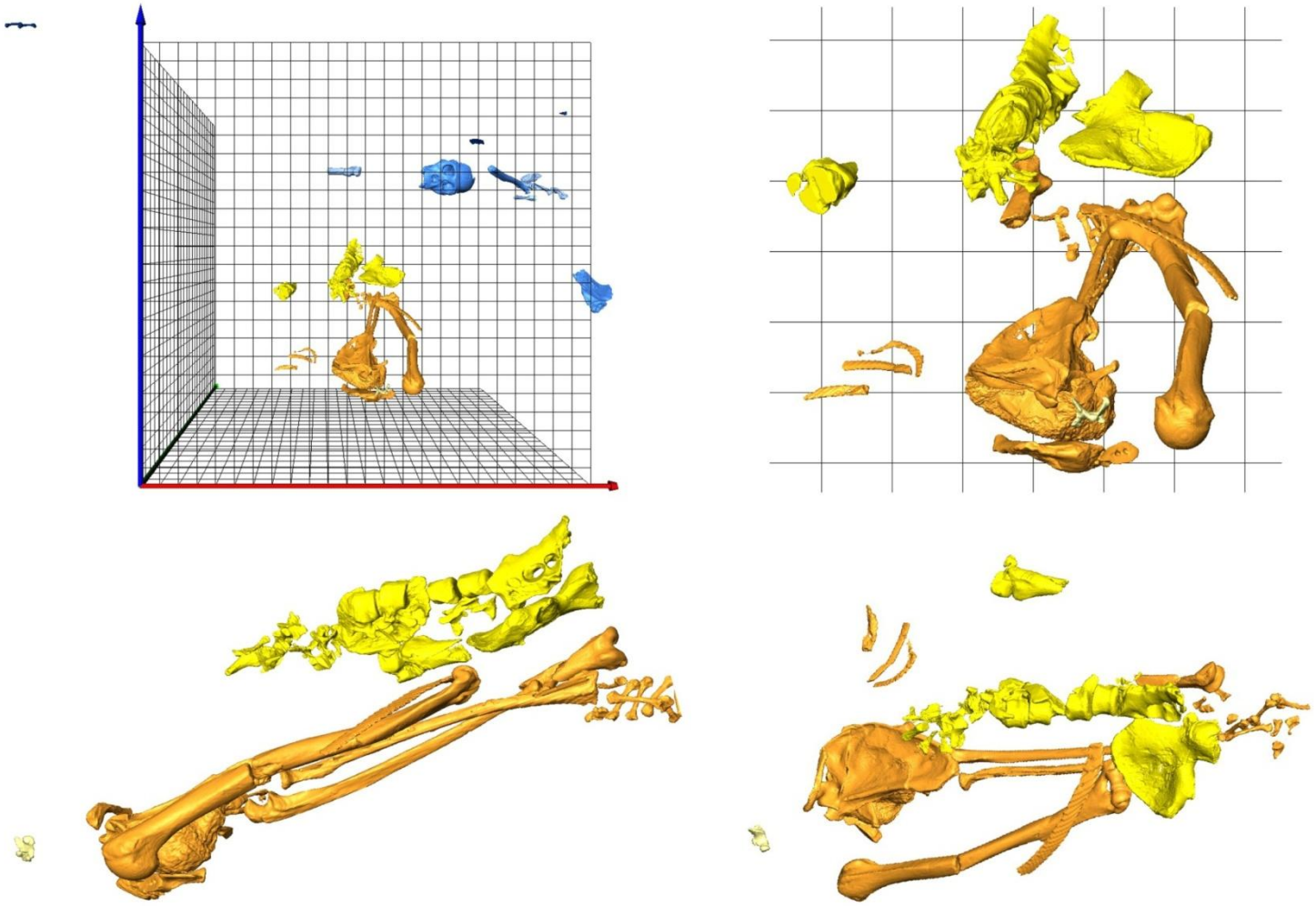
**Hypothesis 2**



Top left: XZ view (from the south); top right: zoom of the XZ view (from the north); bottom left: YZ view (from the east); bottom: XY view (from the top).

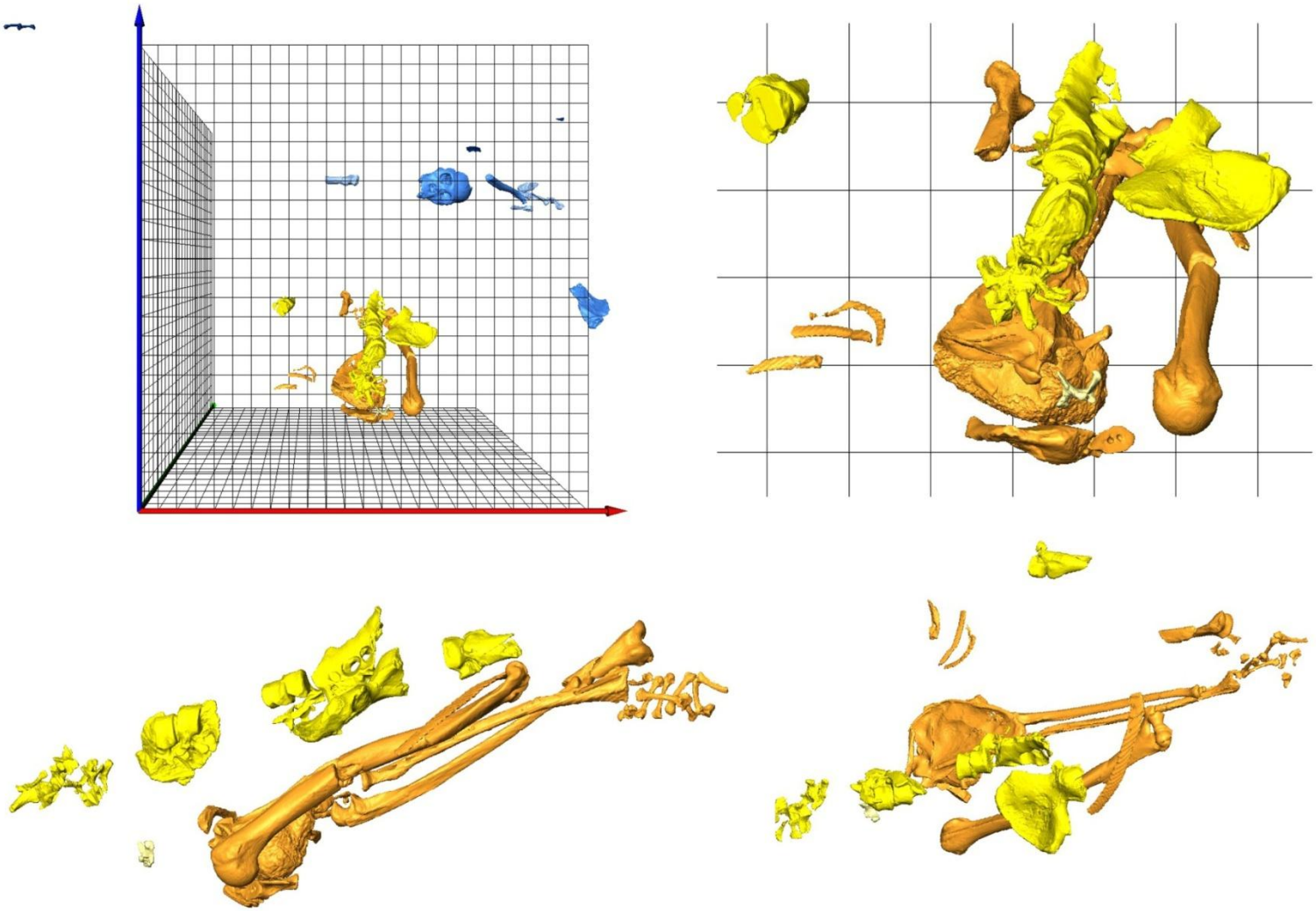
REFITTING MH2 THORACIC BLOCKS 1 and 2

**Hypothesis 1**



Top left: XZ view (from the south); top right: zoom of the XZ view (from the north); bottom left: YZ view (from the east); bottom: XY view (from the top).

**Hypothesis 2**



Top left: XZ view (from the south); top right: zoom of the XZ view (from the north); bottom left: YZ view (from the east); bottom: XY view (from the top).

**Appendix 6**. Estimation of the Minimum Number of Individuals (MNI) accumulated through a death trap scenario at Malapa

| **Species** | **Individuals/Specimens** | **MNI** |
|---|---|---|
| Hominins | MH1 | 1 |
| | MH2 | 1 |
| Bovid class II | Various elements in articulation, partial skeleton, 3 antimeric sets of bones, one near complete foetus in articulation | 2 |
| Bovid class III (*Tragelaphus* sp.) | Various elements in articulation, partial skeleton, 5 antimeric sets of bones | 1 |
| Small carnivore (possible genet) | Complete upper body-part in articulation and near articulation | 1 |
| Lagomorph (*Lepus* sp.) | Articulated bones, 3 antimeric sets of bones | 1 |
| **TOTAL** | **-** | **7** |